Studies on the breeding biology and population dynamics of the great skua (catharacta skua brűnnich)

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STUDIES ON THE BREEDING BIOLOGY AND POPULATION DYNAMICS OF THE GREAT SKUA (*Catharacta skua* Brünnich)

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ABSTRACT

The history and breeding biology of the North Atlantic Great Skua Catharacta skua skua Brünnich was examined to determine its status in seabird communities, and to find reasons for current population increases.

A variety of colony census methods are critically compared. Changes in colony sizes in Iceland, Faroe and Britain, which appear to be genetically isolated populations, are documented in detail. Evidence is presented suggesting that the Great Skua first colonised the northern hemisphere around 1300 AD.

Ringing recoveries are analysed to examine movements of known-age birds through the year. Causes of mortality are examined in relation to age and area of recovery. Attendance of prebreeders is described.

A computer model is used to estimate energy requirements of Great Skua and other seabird populations. Model precision is examined using sensitivity analyses and a Monte Carlo method.

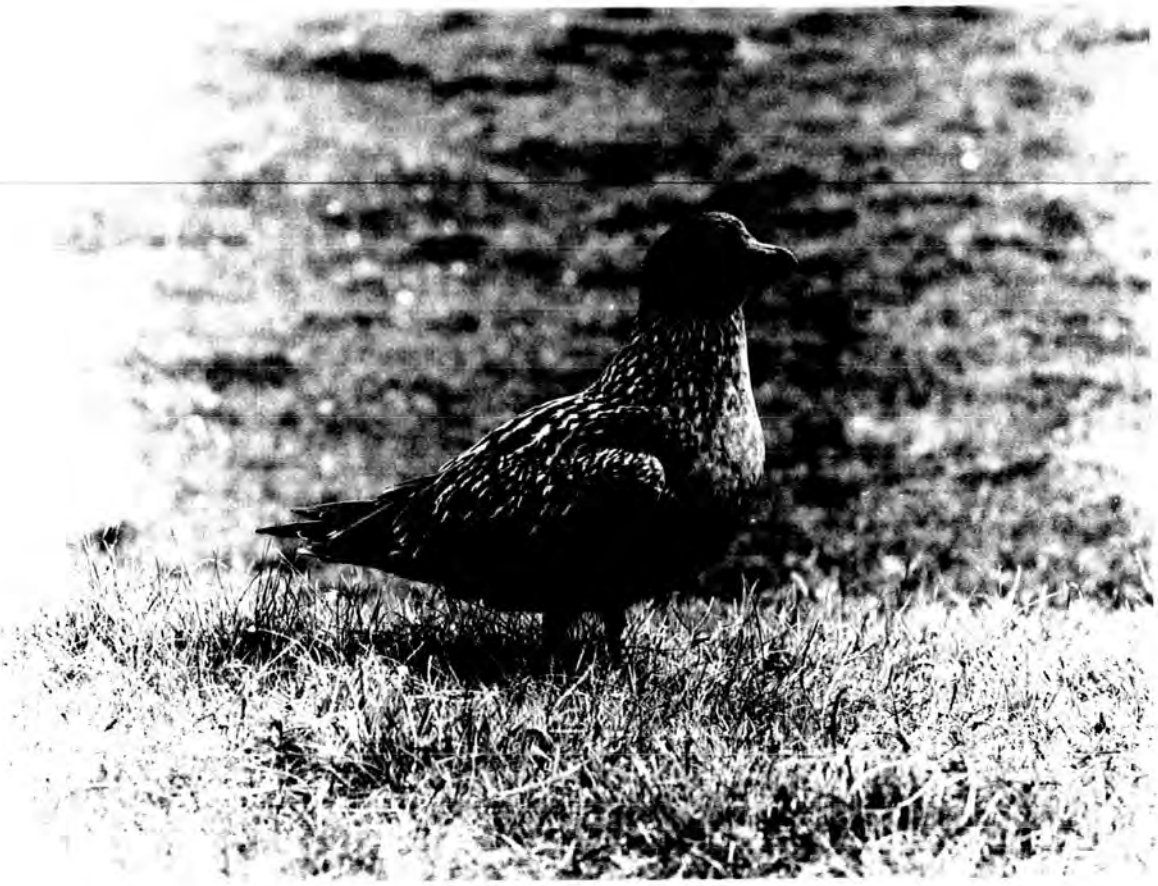
Seasonal variations in Great Skua diet were examined by analyses of pellets and regurgitates. Time budgets of breeders and prebreeders were compared, and food preferences determined. The relative importance of predation and kleptoparasitism as feeding techniques, and their effects on other species are discussed.

Methods were developed to classify eggs into first or second laid, and to estimate hatching dates from egg densities. Rates of chick growth were studied in relation to hatching status and date. Conversion tables were prepared to age chicks and to determine an

index of body condition from measurements. Pesticide and pollutant concentrations were examined in adults and eggs, as were the influences of these, of age, experience, nest density and food availability, on breeding success.

Effects of interactions with nesting Arctic Skuas were investigated, and factors influencing success of kleptoparasitic chases by both species were determined.

Adult and first year survival rates were estimated and rates of colony increase compared. Future population changes are discussed speculatively.



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Fieldwork in 1973, which comprised an undergraduate research project, was supported by Durham University and supervised by Dr. J.C. Coulson. Funds from the Scottish Ornithologists' Club and the Seabird Group supported fieldwork in 1974. Between October 1974 and September 1977 I was supported by a research studentship

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CONTENTS

INTRODUCTION

The only major works on the breeding biology of the North Atlantic Great Skua (Catharacta skua skua) are Bayes, Dawson and Potts (1964) on food and feeding in the Faroes, Perdeck (1960) on behavioural postures, and Perry (1948) on the breeding statistics of the Noss colony through the season of 1946. In contrast, a number of detailed studies of the closely related southern hemisphere races have been undertaken. Also, paradoxically, the numbers of Great Skuas in the entire North Atlantic population, distributed between Iceland, the Faroes and Britain, have been more precisely documented over the last 200 years than those of any other seabird population in the North Atlantic, with the possible sole exception of the Gannet (scientific names of all species mentioned in the text are given in appendix 1.). Large numbers of Great Skua chicks have been ringed, giving both recoveries through the annual cycles of known-age birds, and samples of known-age breeding birds. For all these reasons, I decided that it would be worthwhile to undertake a study of Great Skua breeding biology.

Foula serves both as the breeding ground of the largest Great Skua colony in the world, and as the venue for annual expeditions from Brathay Hall, so it was a natural choice as the main fieldwork site. Brathay first visited Foula in 1956, and have sent at least one expedition there every summer since. The early expeditions were designed to broaden the minds of young men selected from industry and schools, but included a group of keen amateur ringers and birdwatchers. Some seabirds were ringed every year, and annual reports of ornithological observations were produced, but no systematic studies were planned. In 1966 Brathay decided to colour ring Great Skua chicks on Foula and Iceland to see if some interchange occurred between colonies. Only a few were ringed, and only a single colour ring used; yellow for Foula

and red for Iceland. In 1968 larger scale colour ringing was begun, using a second colour to denote year of ringing, and between 1000 and 2000 chicks have been ringed by colony and by cohort in each subsequent year in Foula and Iceland. In 1969 a formal fieldwork programme was instigated on Foula, and annual reports published (Mawby 1969, 1970, 1972, 1973, Furness 1974b, 1976, 1977a) but expeditions to Iceland continued to be informal, with chick colour ringing the only annual commitment. The main activities of the Foula programme are the annual collection and recording of bird corpses attributed to Great Skua predation, estimates of chick numbers by capture-recapture, and mapping and census of Great Skua, Arctic Skua and Arctic Tern colonies.

Foula is a small island, situated 22 km west of the nearest point of Shetland mainland. It is 5 km from north to south and 4 km from east to west, but has the second, third and fourth highest peaks in Shetland and the highest sheer cliff in Britain. Most of the island is composed of old red sandstone, with a small area of highly metamorphosed pre-Cambrian strata in the extreme nort-east (Mykura 1976). Parts of the low-lying eastern side of the island have been fenced in and cultivated, but outside these areas, now inhabited by only 25 permanent residents, the land is covered with peat, often of considerable depth. Drainage is poor, resulting in many small pools and areas of damp and marshy ground. Access to Foula is difficult, and accommodation very limited, so the island is undisturbed by tourists. Residents rarely leave the two infield cultivated areas, so the wildlife of the island is undisturbed, as it has been for many years.

The aim of this thesis is to elucidate details of the breeding biology of the Great Skua and to interpret the documented changes in numbers, and the interactions with other species in relation to these data.

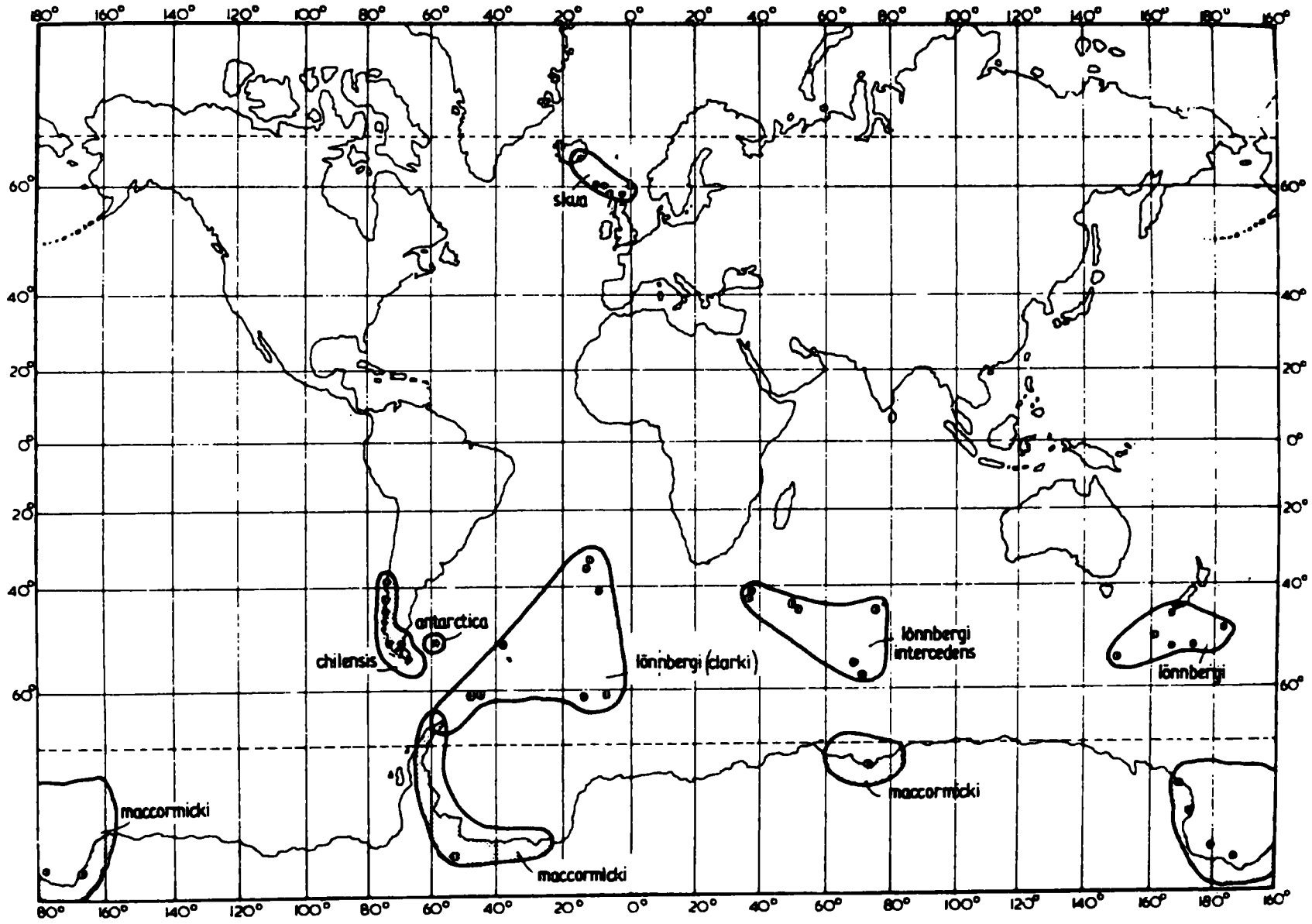
Fisher and Lockley (1954) consider the suborder Lari to be of northern origin; they suggest that the Great Skua originally came from the north, but colonised the south, differentiated there into several distinct taxa, while the ancient northern stock became extinct. The recolonisation of the North Atlantic by the Great Skua they believe to be a fairly recent development (geologically speaking). They consider that the differentiation of the Great Skua superspecies is sufficient to warrant a distinct genus, separated from the three small skuas (Stercorarius), and called Catharacta. This distinction seems sensible, particularly as two of the southern taxa have now been shown to breed sympatrically without hybridisation on the Antarctic peninsula, so should be considered separate species; Catharacta maccormicki, the South Polar Skua of the Antarctic continent and Catharacta skua lönnbergi, the Brown Skua of the sub-Antarctic islands and the Antarctic peninsula (Salomonsen 1976). The North Atlantic Great Skua C. s. skua is most similar to the Great Skuas of Tristan da Cunha and Gough Island, the nearest southern breeding area, and it seems possible that the colonisation of the north occurred from there. The breeding ranges of these taxa are shown in figure 1.

This thesis deals only with the North Atlantic Great Skua populations in Iceland, Faroe and Britain, and concentrates primarily on the British population, with all detailed fieldwork based on the colony on Foula. After discussing the merits of methods used to census Great Skua colonies, the changes in colony sizes in all three countries are examined and the evolutionary relationship between the populations is inferred. The subsequent sections deal with aspects of breeding biology, relationships with other species and population dynamics. In attempting to cover a large number of aspects of Great Skua biology many topics have been dealt with in less detail than they deserve and,

of necessity, many of the problems superficially examined and not resolved.

All statistical tests used in this thesis are taken either from Sokal & Rohlf (1969), using statistical tables in Rohlf & Sokal (1969), or were computed using the Statistical Package for the Social Sciences (SPSS) available in the NUMAC computer unit. For statistical methods, limitations and assumptions in SPSS programmes see Nie, Hull, Jenkins, Steinbrenner & Bent (1975).

Figure 1. Distribution of Catharacta taxa; the Great Skua C. skua skua, the Brown Skua C.s. lonnbergi, C.s. antarctica, C.s. chilensis, and the McCormicks, or South Polar Skua C. maccormicki, (from Salomonsen 1976).


skua
antarctica
chilensis
lönnbergi (clarki)
lönnbergi intercedens
lönnbergi
maccormicki
maccormicki
maccormicki

SECTION 1

COLONY CENSUS METHODS

Methods

Most counts of Great Skua colony sizes have been made at colonies containing less than 100 breeding pairs, so they may be presumed to be fairly precise. Only recently have a few colonies become large enough to make counting difficult. At these colonies the following techniques have been employed:

1. Rough and subjective estimation of the number of breeding pairs, after a general examination of the colony. This method is obviously open to considerable inaccuracies. Unless stated otherwise by the author, I have assumed that this method was used when interpreting published counts of Great Skua colony sizes.
2. Belt transects by observers, walking slowly through the colony, counting nesting pairs as they react to intrusions to their territory by repeatedly diving at the intruders. This method is stated by Cramp *et al.* (1974) to be the best one to use to count Great Skuas.
3. Repeated searching of the colony area to locate and mark all the nests with eggs, or broods of chicks, in the colony.
4. Direct counts of territory holding individuals or pairs, from a distant point so that the birds being counted are undisturbed. Large colonies are divided into convenient subsections, each of which is counted separately.
5. Determination of nest densities in sample plots, and of the total area occupied by the colony, allowing a calculation of the total number of breeding pairs in the colony from these values.
6. Capture-recapture estimation of the number of chicks in the colony, and determination of the mean number of chicks raised to a ringable

age by each pair of Great Skuas, allowing a calculation of the number of breeding pairs required to produce the estimated number of chicks present.

The first four methods have been used frequently, while the last two have not been attempted at any colony other than Foula.

Subjective estimation

It is difficult to measure the accuracy of subjective assessments of colony size, since these have rarely been made at the same colony in the same or successive years, by independent ornithologists. Four pairs of counts may be compared; these were all made at the Foula colony. The two year interval between two of the pairs of counts may be ignored as changes in numbers of breeding pairs occur over long time periods; the high adult survival rate, site fidelity and low recruitment rate of the Great Skua precludes large fluctuations in numbers breeding from year to year. These subjective estimates differ by up to 100% (table 1), so it is clear that large colonies require a careful census.

Counting aggressive territory-holders

Counting pairs as they react to the observer entering their territory, the currently recommended technique, requires several assumptions to be satisfied. All territories entered must be occupied by at least one of the adults, at least one adult in each territory must be sufficiently aggressive to mob the intruding observer, and the observer(s) must cover the colony sufficiently thoroughly to enter every territory, without entering and counting territories more than once. This technique has been used by a number of expeditions

Table 1. Differences between subjective estimates of the number of breeding pairs of Great Skuas on Foula, made by different ornithologists.

Author	Year	Estimated number of breeding pairs	Percentage difference $\frac{100x(larger-smaller)}{smaller}$
Evans & Buckley (1899)	1887	60	
			40%
Barrington (1890)	1889	84	
Clarke (in Evans & Buckley (1899))	1890	40	
			100%
Barrington (1890)	1890	80	
Raeburn (1891)	1891	60	
			67%
Clarke (1892)	1891	100	
Dickens (1958)	1956/58	500	
			100%
Perdeck (1960)	1958	1000	

to Hermaness, Unst (Eggeling 1958, Dott 1967, Albon et al. 1976). Albon et al. (1976) found 739 nests with eggs or broods of young, but only elicited territorial reactions from adults in 467 of these territories. In a further 31 territories at least one adult was seen to be present, but 241 nests or broods were located in territories which appeared not to have an adult present. They concluded from these data that this technique will seriously underestimate colony size because many territories will not contain adults when entered, although aggression was recorded in 94% of the territories in which adults were seen to be present. However, 24 hour hide watches of individually colour-ringed Great Skuas in territories on Foula showed that at least one of the pair is present at the territory all the time to guard the chicks. Only towards the end of the breeding season, when food may become very difficult to obtain, do the few pairs with still unfledged chicks both leave the territory to forage (section 5). It seems more likely that the 241 territories recorded by Albon et al. (1976) as empty, were occupied by an adult or adults which were less aggressive than normal, so that they left the territory when the census team arrived, rather than attack them. Great Skuas are much less aggressive towards a group of people than towards a single human intruder, and as the census team used to cover the Hermaness colony contained between six and eight people, it might be expected that a number of birds or pairs would chose to retire rather than attack. The aggressive behaviour of adult Great Skuas towards an intruding human was examined semi-quantitatively on Foula in 1975 and 1976. Aggression scores were noted on a 1-5 scale (table 2) at each visit to every nest in particular areas of the colony, and on alternate days through the 1976 season at seven chosen territories. The aggression scores tended to be slightly lower when only one adult was present, so observations

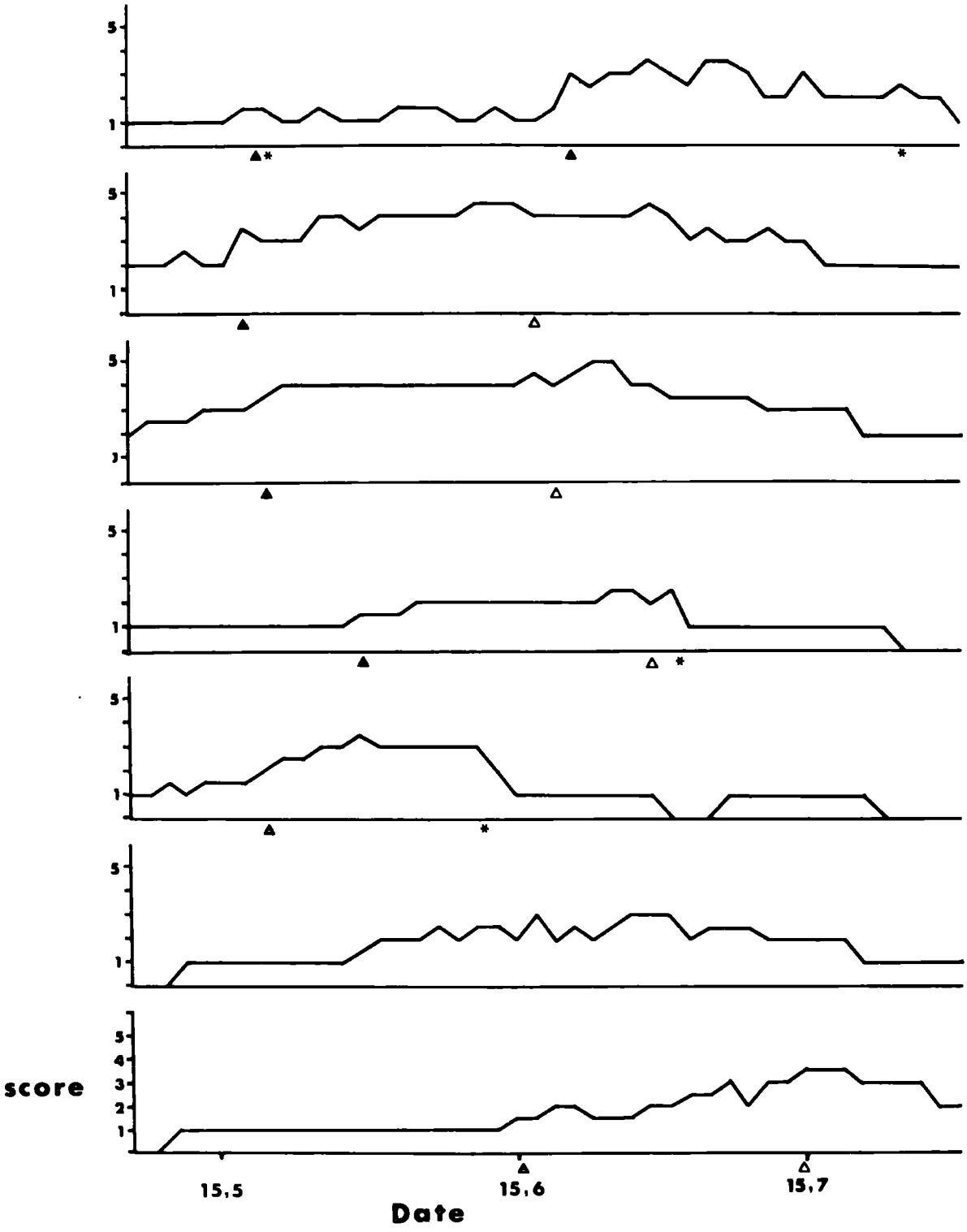
were only recorded if both adults were present. In every case the aggression score of the more aggressive bird was recorded. The less aggressive bird tended to follow the attacks of its mate, but pulled up sooner. This contrasts with the attacking behaviour of Arctic Skuas, where both birds usually attack as a coordinated pair, diving at the intruder from opposite sides.

Table 2. Values of the aggression score used to quantify the strength of territorial defence by Great Skuas.

Score	Definition of the score value
1	left territory when disturbed by single observer
2	circled above territory but did not swoop at observer
3	swooped at observer but rarely or never hit
4	swooped regularly, hitting occasionally
5	swooped regularly, hitting almost every time

To determine seasonal trends in the aggression score the seven pairs examined in detail were scored on a nine-point scale including $\frac{1}{2}$ values between the five scores in Table 2. Clear seasonal trends were shown, although these are obviously determined by the stage of breeding of the pair rather than the calendar date (fig 2). Aggression increases immediately after egg-laying, tends to increase slowly towards hatching, with an upward jump as the chicks begin to vocalise from inside the egg two to three days before hatching, then declines slowly as the chicks grow. The loss of eggs or chicks resulted in an immediate reduction in the aggression score, while a pair with addled eggs slowly became less aggressive as they exceeded the normal

Figure 2. Aggression scores of Great Skua pairs on Foula in 1975 at two day intervals through the breeding season. Laying dates are marked ▲ . Loss of the clutch or brood is marked * . Hatching dates are marked △ .


score
5
4
3
2
1
15,5
15,6
15,7
Date

incubation period. A pair which held territory but did not lay a clutch showed a slow increase in aggression up to the end of June, possibly facilitated by the increasing aggression of their neighbours, then the aggression score declined through July, also following trends in neighbouring pairs. The aggression scores tended to be very consistent from day to day, and, as the change in the score during the middle of the incubation period was small in every case, the median score obtained from the visits to each of the study nests over the middle 20 days of incubation was used in all analyses relating to the level of aggression of each breeding pair. These median scores, from pairs in each study area in 1975 and 1976 are given in table 3.

Table 3. Median aggression scores obtained at each nest in the study areas in 1975 and 1976.

Area	Year	Number of nests	Median aggression score 1	2	3	4	5	Mean	S.D.	S.E.
Flick	1975	184	11	43	53	63	14	3.141	1.051	0.078
East	1975	261	11	58	96	73	23	3.149	1.002	0.062
East	1976	372	25	59	172	98	18	3.067	0.939	0.049
Ristie	1975	32	2	4	16	9	1	3.094	0.893	0.158
Ristie	1976	32	3	9	12	7	1	2.812	0.998	0.176
ALL AREAS.....		881	52	173	349	250	57			
% each score..		100	6	20	40	28	6			

It is quite likely that most birds with aggression scores of 1 or 2 will not be noticed during belt transects determining numbers of territory-defending individuals or pairs, particularly if large numbers

of people are used in census teams or the census is not carried out during the middle or late incubation period. Some individuals with aggression scores of three may also be missed as many of these make only half-hearted swoops towards intruders, which may be misinterpreted as the initial swoops of a bird occupying a territory ahead of the census team. This error could lead to a total underestimation of the number of breeding pairs by over 25% (aggression scores 1 and 2 include 26% of all territories). It is also unlikely that every territory will be entered by the census team, however carefully the transects are carried out, while some pairs will not have laid, will have lost eggs but not yet replaced them, or will have chicks which require little defending, and will therefore be showing low aggression scores at the time of the census. For these reasons, it is not surprising that Albon et al. (1976) failed to elicit aggressive territory defence from 272 of the 739 territories (37%) where nests or chicks were found. Although this technique has been recommended as the standard one for censuses of this species, it is clear that acceptable results are not obtained, and as it also requires a large expenditure of manpower to cover an entire colony, it should be rejected as an unsuitable method.

Marking nests

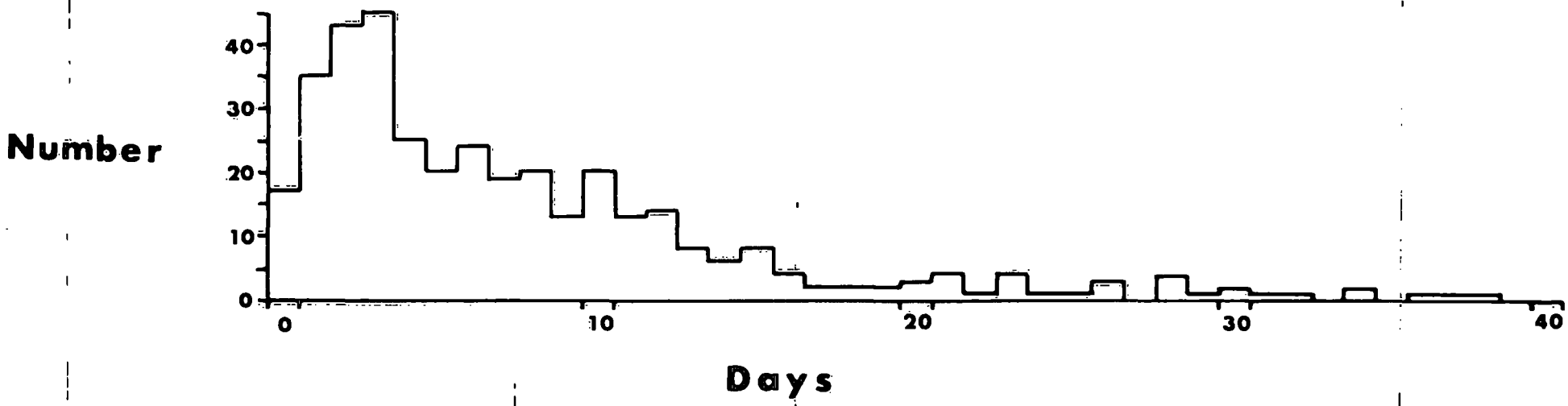
Studies using the previous method also marked nests as they were found, in an attempt to obtain a second estimate of the number of breeding pairs. Searching for nests has also been used on Noss by Perry (1948) and Kinnear (1974), and on Foula, over parts of the colony only, in this study. Great Skuas are surprisingly timid when incubating. It is unusual for an incubating bird to remain on the eggs when a human comes into sight within 200 metres, although the same

individual may strike the human repeatedly if he enters the bird's territory. Because of their timidity, nests must be found by random search within territories. Aggression does not seem to increase as the nest is approached; very little nest material is used, so finding the cryptic nests is time-consuming. Clutch initiation in Britain may occur on any date between 1 May and 25 June (section 5) and losses of eggs may result in replacement clutches being laid, sometimes in a fresh nest, so the determination of numbers of breeding pairs from numbers of nests found is not straightforward. The difficulty in finding nests also makes it difficult to use this technique effectively in colonies containing over 500 breeding pairs. As some clutches will have hatched before the last clutches have been laid, it is impossible to census a colony by nest-counting over a three or four day period; nests must be marked through the entire laying period. Once chicks have hatched, they are so mobile that it is often impossible to distinguish between chicks belonging to different territories and siblings, so counts cannot be based on locating chicks. Up to 25% of clutches may be lost before hatching, and some of these are replaced. Clutches which disappear shortly after laying may easily be missed, while repeat clutches may be mistaken for first clutches. In an intensive nest marking study in part of the Foula colony in 1976, daily searches for nests and chicks were made between 1 May and 1 August. The interval between clutch initiation, estimated from observed hatching dates or egg densities, and finding of the nest varied from less than one minute up to 32 days (i.e. nests in which the second egg was hatching), and a further six breeding pairs were located by finding chicks, aged between one and 17 days old, although the nests from which they hatched had not been found. The distribution of intervals between clutch initiation and nest finding (table 4, figure 3) would follow a Poisson distribution

Table 4. Days between clutch initiation and nest finding for the 372 nests in the area "East" on Foula in 1976.

Days	Frequency	Cumulative frequency	Cumulative percentage
0	17	17	4.6
1	35	52	14.0
2	43	95	25.5
3	45	140	37.6
4	25	165	44.4
5	20	185	49.7
6	24	209	56.2
7	19	228	61.3
8	20	248	66.7
9	13	261	70.2
10	20	281	75.5
11	13	294	79.0
12	14	308	82.8
13	8	316	84.9
14	6	322	86.6
15	8	330	88.7
16	4	334	89.8
17	2	336	90.3
18	2	338	90.9
19	2	340	91.4
20	3	343	92.2
21	4	347	93.3
22	1	348	93.5
23	4	352	94.6
24	1	353	94.9
25	1	354	95.2
26	3	357	96.0
27	0	357	96.0
28	4	361	97.0
29	1	362	97.2
30	2	364	97.8
31	1	365	98.1
32	1	366	98.4
34	2	368	98.9
36	2	370	99.5
38	1	371	99.7
48	1	372	100.0

Figure 3. Number of days between the laying of the first egg and finding of the nest, showing the tendency for a small number of nests to be much more difficult to find than most.


Number
40
30
20
10
0
0
10
20
30
40
Days

if all nests were equally difficult to find, resulting in a random finding process. For the 372 nests studied, the mean interval between clutch initiation and nest finding is 7.73 days, with a variance of 58.11 days. This gives a variance to mean ratio of 7.52, indicating that the distribution of intervals deviates very considerably from a Poisson Distribution. Clearly, some nests are far more difficult to locate than others. However, the study area was covered thoroughly, and it is improbable that any pairs bred without being detected. Three pairs were found which held territories in the study area but either did not lay, or lost their eggs very early in the incubation period, so the breeding population of the study area was between 372 and 375 pairs. In less detailed studies, where the intention is to determine the number of breeding pairs rather than to obtain detailed nest histories, the main errors would arise from losses of clutches before nest location, failure to locate nests, and the counteracting error of counting replacement clutches as first clutches. The numbers of lost clutches which were replaced in the three study areas examined in 1975 and 1976 are shown in table 5.

The percentage of clutches lost was positively, and highly, correlated with nest density. Nest density in the Flick area is the highest recorded for Great Skuas in any colony, so it may be expected that the 26% of clutches lost will be a maximum value. The proportion of lost clutches which are replaced varied between 11 and 32%. Probability of replacement is determined by the date of egg loss; only clutches lost before 11 June are likely to be replaced (table 6). Taking the extreme values; if 26% of clutches were lost, and 32% of these were replaced, and all replacement clutches were mistakenly identified as first clutches, then the number of breeding pairs would be overestimated by 8%. In most colonies, one might expect no more

Table 5. Numbers of clutches lost and replaced in study areas on Foula.

Area	Year	Clutches found	Clutches lost	Clutches replaced	Percentage: lost	Percentage: replaced
Ristie	1975	32	0	-	0	-
	1976	32	0	-	0	-
Flick	1975	184	47	15	26	32
East	1975	261	18	5	7	28
	1976	372	18	2	5	11

Table 6. The number of lost clutches which were replaced in relation to the date of clutch loss; all three areas in 1975 and 1976.

Date lost	Number lost	Number replaced	% replaced
21.5 - 31.5	1	1	100
1.6 - 10.6	9	6	67
11.6 - 20.6	10	0	0
21.6 - 30.6	12	0	0
1.7 - 10.7	4	0	0

than 8% of first clutches to be lost, and only 20% of the lost clutches to be replaced, giving a 1.6% overestimate of the number of breeding pairs.

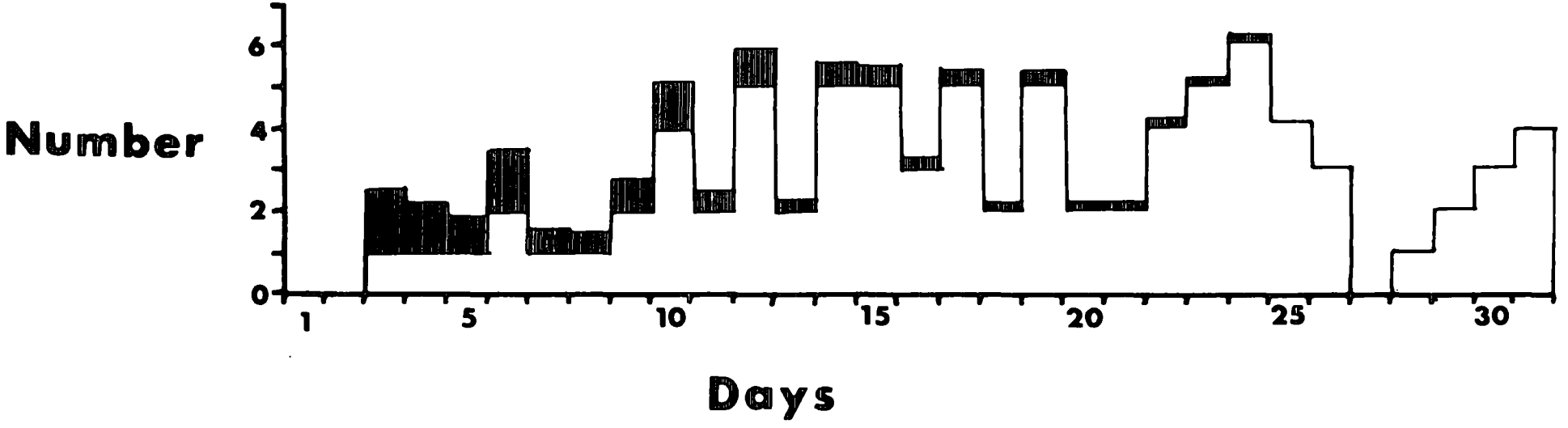
A tendency to underestimate numbers arises from the possibility of missing clutches which are lost soon after laying. The distribution of periods between clutch initiation and clutch loss for the 83 clutches lost from 881 nests marked in three areas in the two years (table 7) suggests that clutch predation tends to occur more in the middle of the incubation period than at the beginning and end. However, it is possible to examine how many clutches were lost before being found by multiplying the number known to be lost by 100, and dividing this by the cumulative percentage of nests found by that stage of incubation (table 7). This calculation suggests that 13 or 14 nests were missed because they would have been robbed before being found, so, in spite of the intensive nature of the study, 14 of 895, or 1.6% of nests, may have been missed.

The distribution of intervals between clutch initiation and clutch loss, even when allowance has been made for nests lost before being found, shows a greater loss rate around the middle of incubation (figure 4). Examination of the seasonal timing of nest losses (section 5) shows that losses are temporally synchronous, depending on food availability rather than parental motivation and/or the stage of incubation. It appears that considerable, but short-lived reductions in food availability in 1975 and 1976 occurred when most birds were in the middle of the incubation period, causing the observed pattern. Availability of abundant food seems to become less predictable through June and July (section 4), so this form of pattern is probably typical. Thus, few clutches will be lost in the early days of incubation, and those which are will probably be lost before 11 June, as 95% of first

Table 7. Numbers of nests known to have been robbed, and the number of nests found used to determine the actual number of nests robbed, including those robbed before being found.

Days after clutch initiation	Number of clutches known to be lost	Cumulative total of nests found as a percentage of those found before hatching	Corrected number of clutches lost
0	0	5	0.00
1	0	14	0.00
2	0	26	0.00
3	1	38	2.63
4	1	45	2.22
5	1	51	1.96
6	2	57	3.51
7	1	62	1.61
8	1	68	1.47
9	2	71	2.82
10	4	77	5.19
11	2	80	2.50
12	5	84	5.95
13	2	86	2.33
14	5	88	5.68
15	5	90	5.56
16	3	91	3.30
17	5	92	5.43
18	2	92	2.17
19	5	93	5.38
20	2	94	2.13
21	2	95	2.11
22	4	95	4.21
23	5	96	5.21
24	6	96	6.25
25	4	97	4.12
26	3	98	3.06
27	0	98	0.00
28	1	99	1.01
29	2	99	2.02
30	3	99	3.03
31	4	100	4.00
32	0	100	0.00
	83		96.86

Figure 4. Number of days between the laying of the first egg and loss of the clutch. Unshaded parts of the histogram are observed data. The shaded areas are added on the assumption that a proportion of the nests which suffer predation will not have been found before they are robbed. The correction is based on the known distribution of intervals between clutch initiation and nest finding (figure 3).


Number
0
2
4
6
1
5
10
15
20
25
30
Days

clutches have been started by this date, so a replacement clutch will probably be produced. If the first clutch is not found before it is lost, and the replacement clutch is counted as a first clutch, then the two errors cancel exactly. The remaining source of error with this method is the problem of finding every nest. Although some nests are much more difficult to find than others (figure 3), the aggression of adults, and the regular spacing of territories, help to suggest where a missing nest may be expected, so that, given time, almost every nest can be found. For the area "East" in 1976, 366 nests were found, and 18 clutches were lost, for which two replacement clutches were laid. Calculation of clutch losses allowing for the time interval between laying and nest finding indicates that three nests may have been robbed before being found, and replacement clutches for these three nests may have been counted as first clutches in the total of 366. A further six clutches hatched before the nest had been found. Thus the number of breeding pairs was 366 + 6 =372. A count of nests would have given 366 + 2 = 368, which is an underestimate by 1.1%. Thus, careful use of this method over the entire clutch initiation and incubation period, from 1 May to 10 July, should give an estimate of the number of breeding pairs to ± 2%. This is by far the best accuracy that can be achieved in the census of Great Skua colonies, and is also compatible with studies of breeding success, phenology and colony organisation. Less precise application of the method would underestimate actual numbers, but probably not by more than a few percent, as only a small proportion of nests prove difficult to find, while the majority can be found within a few days of laying (figure 3). The main limitation is the extended time period over which clutches may be laid, and therefore over which the study must be extended.

Direct counts of territories

Although thorough searching for nests will give a very precise estimate of the number of breeding pairs in small or moderately sized Great Skua colonies, colonies containing over 500 breeding pairs require a prohibitive amount of searching effort. Furthermore, that method requires a continuous study through the entire incubation period, so that only one colony can be counted per observer per year. A method which requires only a few days of fieldwork at each colony is still required for routine monitoring of changes in Great Skua numbers, but this method must give more accurate results than provided by either methods 1 or 2. This is provided by direct counts of territories occupied by individuals or pairs, made from a distant point so that the birds being counted remain undisturbed.

Great Skuas prefer to nest on high ground, but avoid slopes, so that all British colonies are on flat or gently sloping surfaces, which can easily be scanned from a distance with binoculars. At least one of the pair remains in the territory at all times from egg laying to shortly before the chicks fledge, and, even before laying, it is very rare for both members of a pair to be away from the territory after the pair has formed in April (Section 5), so it is possible to count the number of breeding pairs in a colony by counting the number of occupied territories on any date between late April and mid-July.

Using this technique, the following errors may arise;

1. Birds which are members of a pair, but not standing close together, may be mistakenly identified as two single birds, each holding a territory. The reverse of this may also occur.
2. Both birds may be absent from the territory, and so not counted.

3. Because Great Skuas are darkly coloured, birds may not be noticed against a peaty or heathery background, or may be hidden by uneven topography.

4. Difficulties in defining divisions between count areas, required if the entire colony cannot be counted from one spot, may result in some pairs being counted twice or overlooked.

5. Counts made before June will not include prospecting birds, which move off the clubs to establish territories in June and July. Counts made after the end of June may miss pairs which have lost eggs and deserted their territory early in the season.

The use of this method in areas of Foula where the number of breeding pairs was later determined by searching for nests, showed that pairs were more likely to appear to be two individuals than vice versa. Most territories contain two adults, but it is usually quite clear that these are paired. Errors 1, 2 and 3 are all likely to underestimate the true number, but of the three, overlooking birds because of their cryptic plumage is the only serious problem. Only 1 or 2% of territories are held by birds which do not breed in that season, and usually only 3 to 10% of pairs lose eggs but do not replace them, and only a few of these pairs desert after egg loss, so these errors, which act in opposite directions, are of a similar and unimportant size. The accuracy of this method is thus dependent on the ability of the observer to notice birds as they stand or sit motionless against a similarly-coloured background. This ability improves with practice, but generally results in counts which fall 5 to 15% below those obtained by searching for nests (table 8).

Direct counting of territories does underestimate the number of breeding pairs, and the bias appears to be greater the larger the area counted (table 8), but the bias is fairly consistent, and a

Table 8. A comparison of estimates of the number of breeding pairs of Great Skuas in parts of the Foula colony by counting occupied territories and by marking nests.

Area	Year	Nests marked	Count of occupied territories	% difference
Ristie	1975	32	30	- 6.2
Ristie	1976	32	32	0.0
East	1975	261	238	- 8.8
East	1976	372	332	-10.8
Flick	1975	184	170	- 7.6

count of 500 territories can be completed in less than five hours, so that even the largest colonies of Great Skuas can be censused in three or four days by one person using this method.

Determination of nest densities and colony area

The limits of a colony can easily be mapped on standard 1:10,000 O. S. maps. If sample areas within the colony are marked, and nest densities within these are determined, then the number of nests in the colony can be estimated, either by multiplying mean nest density by total colony area, or bu subjectively dividing the colony into sections of differing nest densities and selecting sample areas to represent each density category (stratified sampling). Nest density in large areas of the Foula colony varies between 50 km^{-2} and 600 km^{-2}, a range of more than an order of magnitude, while 5000 nests km^{-2} may be

found over small areas at the edges of club sites (Furness 1974a), giving a range of two orders of magnitude. This range makes the determination of mean nest density liable to large standard errors, so that useful estimates of the number of breeding pairs cannot be obtained without stratified sampling. As few Great Skua colonies contain over 1000 breeding pairs, the effort required to undertake stratified sampling approaches that of marking every nest, so there is little to be said for this method.

Capture-recapture estimation of chick numbers

A large proportion of the chicks reared on Foula each year are ringed and colour ringed, and, as a byproduct of this intensive ringing programme, an independent estimate of the number of breeding pairs can be obtained using capture-recapture estimates of the number of chicks in the colony and estimates of the number of chicks raised to a ringable age per breeding pair. Because both chick production per pair and ringing efficiency may be correlated with nest density, the colony was divided each year into five subjective density categories. Chicks were ringed during uniform transects through every area in turn, then one of the areas from each density category was selected to give an estimate of ringing efficiency by recapture of chicks, giving the proportion which had been ringed. As a proportion of pairs may have eggs or chicks which were too young to be ringed, these were also counted, and the estimated number of ringable chicks was further corrected to allow for the number of eggs and young chicks, assuming that all of these would survive to become ringable chicks. In practice only a small proportion of pairs have eggs or small chicks when ringing is undertaken, so errors arising from this correction will be small.

These calculations are shown for the years 1969 - 1973 (table 9). Measurement of the total area of each density category allows estimation of the number of chicks km^{-2} in each category. This calculation clearly supports the subjective density divisions. However, there is no detectable relationship between nest density and ringing efficiency (table 10); $F_{4,16} = 1.10$, ns, or heterogeneity of ringing efficiency between years, $F_{4,16} = 0.445$, ns, but chick production per pair is inversely related to nest density (section 5) so the colony must be density-stratified to allow chick numbers to be converted to numbers of breeding pairs.

The main assumption required of capture-recapture techniques is that sampling should be random or uniform, with an equal probability of capture for every individual, both in initial ringing and in subsequent recapture. Recapture is carried out within two or three days of the initial ringing, so that mortality between occasions is negligible, while no immigration or emigration occurs due to the territorial nature of the species. To allow a detailed analysis of the validity of capture-recapture techniques to estimate Great Skua chick numbers, the area Hamnafield was chosen for initial ringing followed by a series of three recaptures over a ten-day period in 1974. A total of 324 chicks were ringed in the initial sample, with subsequent samples of 57, 98 and 101 chicks. These data were used to determine the validity of the random sampling assumptions and the confidence interval of chick number estimates using different computational methods. Possible deviations from randomness in the sampling of Great Skua chicks are;

1. Uneven sampling of areas (spatial heterogeneity).
2. Age-related differences in chick catchability.
3. Behavioural differences between individuals of the same age.

Spatial randomness of recapture was examined by dividing the area

Table 9. Capture-recapture estimates of the number of Great Skua chicks in the density categories on Foula 1969 - 1973.

Year	Category	Density category					Total
		1	2	3	4	5	
1969	area (km^2)	2.86	1.33	1.70	1.05	0.71	7.65
	chicks ringed	828	289	312	71	39	1539
	% ringed (est.)	60	48	48	47	49	
	% too small	0	0	0	0	0	
	number chicks	1380	600	650	150	80	2860
	chicks km^{-2}	483	451	382	143	113	374
1970	area (km^2)	2.86	1.33	1.70	1.05	0.71	7.65
	chicks ringed	496	319	240	72	35	1162
	% ringed (est.)	49	83	46	75	33	
	% too small	26	16	24	14	18	
	number chicks	1280	447	648	110	125	2610
	chicks km^{-2}	448	336	381	105	176	341
1971	area (km^2)	1.86	2.77	1.38	1.35	0.49	7.85
	chicks ringed	637	567	209	184	19	1616
	% ringed (est.)	58	39	67	55	33	
	% too small	11	2	17	4	10	
	number chicks	1319	1483	365	347	64	3578
	chicks km^{-2}	709	535	264	257	130	456
1972	area (km^2)	1.86	2.77	1.38	1.35	0.52	7.88
	chicks ringed	606	736	220	143	28	1733
	% ringed (est.)	53	62	46	68	60	
	% too small	10	24	20	18	0	
	number chicks	1257	1482	574	248	47	3608
	chicks km^{-2}	676	535	416	184	90	458
1973	area (km^2)	2.34	2.29	1.79	1.01	0.47	7.90
	chicks ringed	494	515	247	87	9	1352
	% ringed (est.)	40	64	52	50	50	
	% too small	20	15	10	10	10	
	number chicks	1544	947	528	193	20	3232
	chicks km^{-2}	660	414	295	191	43	409

Table 10. Great Skua chick ringing efficiency in relation to nest density and the year of ringing.

		Density Category					
		1	2	3	4	5	Total
Year	1969	60	48	48	47	49	252
	1970	49	83	46	75	33	286
	1971	58	39	67	55	33	252
	1972	53	62	46	68	60	289
	1973	40	64	52	50	50	256
	Totals	260	296	259	295	225	1335

into five geographical sections, each with a similar number of chicks ringed in them. Between section heterogeneity was then examined using a chi^2 test (table 11).

Table 11. Chi^2 test of spatial heterogeneity in recaptures of ringed chicks.

Recapture number	X^2 value	degrees of freedom	Probability level
1	4.283	4	$0.5 > p > 0.1$
2	6.124	4	$0.5 > p > 0.1$
3	11.276	4	$0.025 > p > 0.01$

Sum of X^2 for recaptures: 21.683 . df = 12, ns.

Recapture 3 may have covered the area unevenly, but recaptures 1 and 2 show no spatial heterogeneity, and the sum of the three independent values of X^2 does not indicate a significant overall spatial heterogeneity in recapture, so it may be assumed that the technique employed usually succeeds in covering the area uniformly, as is intended, or randomly, as required by the methodology. The four samples were taken by different groups of people, so it is most unlikely that all four samples suffered from the same pattern of patchy coverage of the area, which could give the same statistical result.

Age-related or behavioural differences in chick catchability can be detected using Leslie's test for nonrandomness (Seber 1973).

Applying this test to the data gives a value of 392.4 for the test statistic T. Applying the normal approximation, required because of the large sample size, $z = 2.6$, $p = 0.01$. Leslie's test shows that there is heterogeneity in the recapture probabilities of chicks in the initial ringed sample. A comparison of the observed and expected number of times each individual was recaptured (table 12), shows that some individuals are more likely to be found than others, but that this deviation from expected, although statistically significant, is small.

Table 12. Observed and expected number of recaptures of each Great Skua chick ringed on the initial ringing date in the Hemnafield area in 1974

Number of times recaptured	Observed	Expected	X^2
0	221	211.70	0.4085
1	81	97.34	2.7429
2	19	14.30	3.3130
3	3	0.66	

$$\text{Total } X^2_{2 \text{ df.}} = 6.4644, p < 0.05$$

This may be partly due to differences in the conspicuousness of chicks of different ages (table 13), although these differences are not statistically significant. Differences in the behaviour of individuals, regardless of age, may be more important; some chicks stand up or run when people approach, while others crouch motionless, or even hide in

the entrance of a rabbit burrow. Overall, the departure from random sampling appears to be small, and, in relation to the precision of the method, can probably be ignored. Any errors arising from unequal catchability would tend to result in the number of chicks in the colony being underestimated.

By using various computational methods, described in Seber (1973), the number of ringable chicks in the Hamnafield area in 1974 was estimated to be 627 (table 14). The 95% confidence interval for this estimate varied depending on the method of analysis, but at best was ± 9%. The three separate recapture samples gave Lincoln Index estimates of 593, 637 and 649 individuals, with standard deviations of 44.5, 45.2 and 80.1 respectively. Thus these simple capture-recapture estimates give 95% confidence intervals of ± 14 to 24% for the number of chicks in the sampled area. Further errors will be introduced by correcting for chicks too small to ring, any bias caused by unequal catchability, and conversion to number of breeding pairs required to produce the observed number of chicks. Even the multiple recapture techniques do not greatly increase precision (table 14).

Clearly, capture-recapture methods are too time-consuming and not sufficiently precise to be suitable for determining Great Skua colony sizes, but do produce a useful independent method of examining chick numbers in colonies or areas of colonies which can be compared with numbers of breeding pairs and chick production statistics independently derived by other methods.

A comparison of Great Skua census methods

Of the six methods examined, four were rejected; counting occupied territories was shown to be the most suitable technique for routine

Table 13. Number of recaptures of individual chicks in relation to their age.

Number of times recaptured	Chick age (days) 5 - 19	20 - 25	26 - 29	30 - 35[1]
0	51	48	67	55
1	27	21	20	13
2	5	5	6	3
3	1	1	1	0
Number of chicks	84	75	94	71
Number recaptures	40	34	35	(19)
Recaptures/individual	0.476	0.453	0.372	(0.268)

1. Chicks aged more than 30 days at ringing are between 40 and 45 days old at the final recapture, so a few of them may have fledged, giving an underestimate of the number of recaptures to be expected for this age group.

2. t-tests between recaptures/individual;

$t_{5 - 19,\ 26 - 29} = 1.407$, ns. so other t-tests cannot give significant differences.

Table 14. Estimates of the number of ringable chicks in the Hamnafield area in 1974 determined by different computational methods.

Method	Estimate of N.	95% confidence limits	Two standard deviations as a percentage of the mean estimate.
Robson & Regier	627	568 - 683	8.9%
Schnabel	627	565 - 696	11.0%
Schumacher	627	559 - 712	13.6%
Peterson (mean)	626	560 - 693	10.7%

census studies, while marking nests gave great precision, but required continuous study through the breeding season. The relative merits of each method are summarised in table 15.

Table 15. A summary of the relative merits of the six census techniques used to determine the number of breeding pairs of Great Skuas in large colonies.

Census method	estimated 95% confidence interval as % of estimate	time-span required for method	number of people required for method	bias in method
Subjective estimation	100%	2 days	1	unknown
Counting aggressive territory holders	25%	4 - 10 days	4 - 8	25% under
Marking nests	2%	80 days	1	none
Direct counts of occupied territories	5%	3 - 4 days	1	10% under
Nest densities and colony area determination	not determined	80 days	1	none
Capture-recapture estimation of chick numbers and estimation of chicks/pair	at least 15%	6 - 20 days	4 - 6	2 - 5% under

SECTION 2

CHANGES IN COLONY SIZES

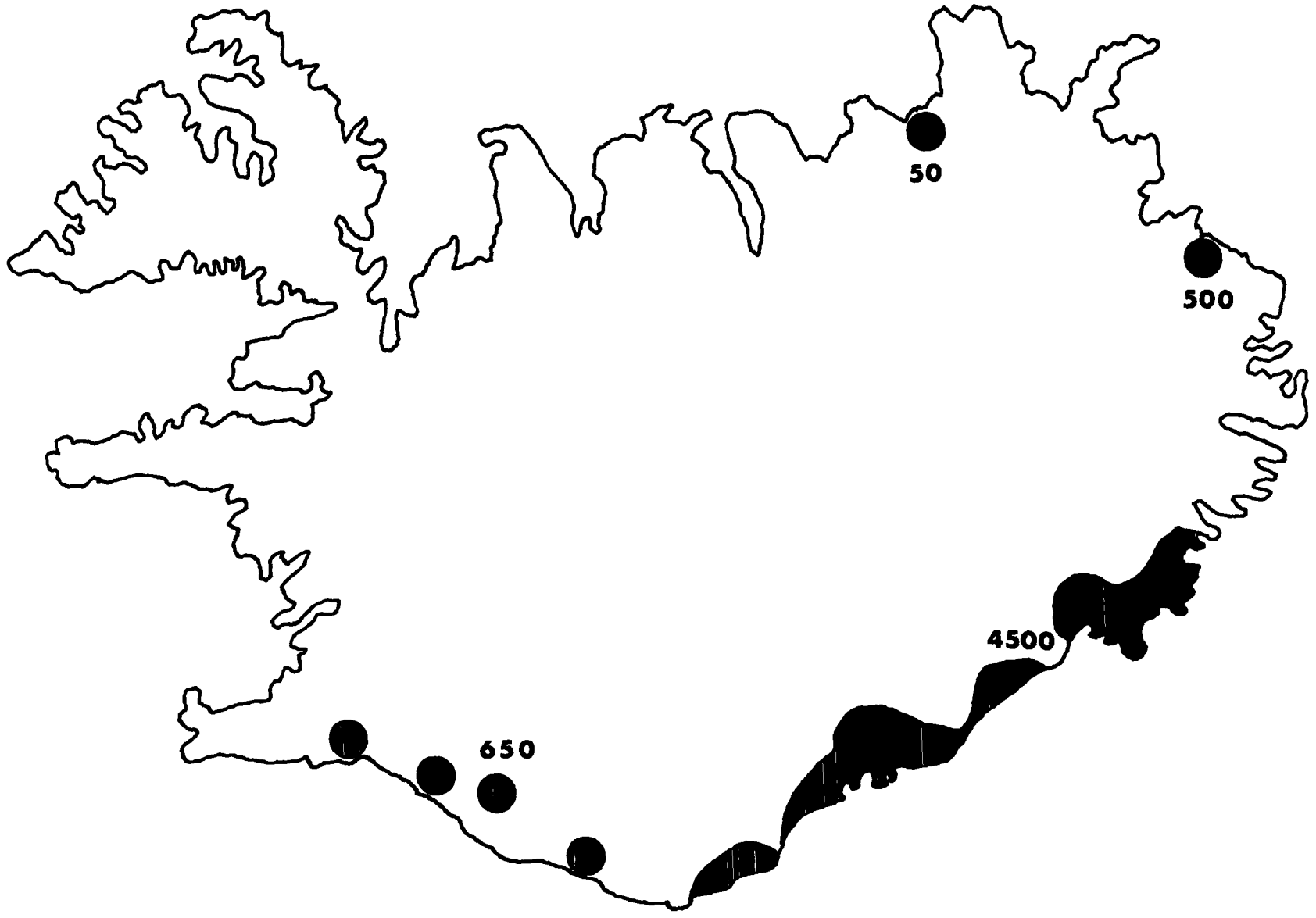
Literature

The literature on population size of the Great Skua may be divided into three distinct categories. Numerous and reliable estimates of the numbers of breeding pairs of Great Skuas in the British colonies are available over the period 1774 to 1976. Slightly less detailed data are available for the Faroe colonies since 1782, while quantitative data for Iceland colonies are lacking before 1954. To elucidate the population trends before these quantitative periods a second category of literature must be consulted; this is the host of works describing and classifying bird species, some of which mention the Great Skua. Thirdly, the implications derived from these data can be supported by an examination of the literature concerning subfossil collections of bird bones, particularly from Stone Age to Viking settlements (the period up to 1000 AD) which can be used to infer the distributions of seabirds during those periods (Clark 1948, Fisher & Lockley 1954), and local literature describing the relationships between crofting communities and the seabirds.

Iceland; quantitative

Gudmundsson (1954) reviewed the status of the Great Skua in Iceland. This appears to be the first and only estimate of the numbers of breeding pairs in each colony in that country. The distribution and numbers given by Gudmundsson are shown in figure 5. The largest colonies are found on the fluvio-glacial plains in South-East Iceland.

Figure 5. Breeding distribution of the Great Skua in Iceland in the 1950's according to Gudmundsson (1954) and Potts (1961). Numbers of pairs in each area are estimated.


50
500
4500
650

In these areas braided glacial streams constantly divide, rejoin and change their courses; the skuas are distributed unevenly over these areas, preferring to nest in localities where short grass or moss carpets have developed. The instability of the substratum leads to changes in colony distribution over the years. This led Dickens (1968) to suggest that numbers of Great Skuas in Iceland had declined between the 1950's and his visits to the two main colonies (Breidamerkursandur and Skeidarursandur) in the 1960's. Annual visits in recent years by Brathay Exploration Group expeditions have shown continuing movements of the colony foci in response to habitat changes; most recently these have included the construction of a road around the southeast coast, channelling of streams, and seeding of large areas of the Breidamerkursandur with grass, and an increased tourist traffic. These changes have improved the habitat for nesting Great Skuas except in areas of human activity, and a shift in nesting distribution has occurred into the Breida area, which led Collier & Stott (1976) to suggest that the Iceland Great Skua population is now increasing; it is likely that this impression is due principally to a redistribution resulting from habitat changes. The continually shifting nature of the nesting habitat has probably resulted in the conflicting reports of declines and increases of Great Skuas in Iceland; it seems probable that little change in numbers has occurred between 1954 and 1976. The ease with which 1000 chicks are ringed each year in the Breidamerkursandur by Brathay expeditions (Collier & Stott 1976) certainly indicates that this colony is not now below the 1500 breeding pairs estimated by Gudmundsson (1954). Nesting density in the Iceland colonies is low; Gudmundsson (1954) cites a value of three pairs Km^{-2} over the entire Skeidararsandur, although he points out that the colony is unevenly distributed over the area.

Britain: quantitative

In 1774 the Great Skua bred at only two sites in Britain, with three pairs at Saxavord, Unst, and six or seven pairs on Foula, but at this time the species was greatly favoured by the islanders of Foula. "In Foula there is a privileged bird, no man will dare shoot it, under the penalty of 16s 8d sterling, nor destroy its eggs: when they meet it at sea, whatever fish they have in the boat Skua always gets a share, and all this out of gratitude for beating off the Eagle, who dares not venture to prey on the island during the whole of the breeding season. Skua is not so strong as the Eagle, but much more nimble: strikes at him without mercy, with such effect that he makes the other scream aloud, and his retreat is so sudden as to avoid all danger from the Eagle" (Low 1879). In spite of the protection afforded to the Great Skua, the colony at Saxavord became extinct before 1861 (Saxby 1874), but that on Foula grew to about 30 pairs by 1804 (Baxter & Rintoul 1953). Great Skuas may have colonised Fair Isle around 1800, as they were reputed to be breeding there in 1804 (Neill 1806), but this author does not appear to have been a very reliable authority; as no other authority gives Fair Isle as a breeding site for this species during the 19th century any colonisation must have been shortlived.

Shortly after 1800 the Great Skuas suffered irregular persecution from visiting skin collectors. Drosier (1830, 1831) was asked by Foula inhabitants to spare the Great Skuas because they drove Sea Eagles and Ravens off the hills, but his visit to Foula was specifically undertaken to obtain specimens of this rarity, and his detailed description of the plumage (Drosier 1830) indicates that his trip was not unrewarded. Because of these killings, the Great Skua population on Foula was still only 30 pairs in 1821 (Vetch 1822). In 1828 one or two pairs began to hold territory at Ronas Hill, Shetland mainland,

(Drosier 1830), possibly discouraged from returning to Foula by the persecution suffered there, and in 1831, three pairs were found to be nesting at Hermaness, Unst (Evans & Buckley 1899). At Hermaness these were protected by the landowner, Dr. L. Edmondston, and increased to 30 pairs by 1850 (Bannerman 1963). Meanwhile, the colony at Ronas Hill, although it had increased to five pairs in 1832 (Evans & Buckley 1899), was totally exterminated by R. Dunn, a taxidermist from Hull (Dunn 1837, Saunders 1880), and persecution on Foula reduced this colony to six pairs in 1850 and three pairs in 1860 (Holbourn MS). In spite of Dr. Edmondston's protection, shooting at Hermaness then escalated, and reduced the colony to only six pairs in 1861 and five pairs in 1871 (Saxby 1874). Foula suffered little persecution over the next two decades, allowing numbers to increase to 15 pairs in 1883 (Tudor 1883). It is possible that Tudor slightly underestimated the number of Great Skua pairs on Foula in 1883, as Evans estimated that there were 60 pairs in 1887. In 1881 one pair bred on Ronas Hill, reestablishing a colony at this site. In the years 1887 to 1899 a number of distinguished Victorian egg and skin collectors visited Foula; each shot numbers of Great Skuas, blamed the others for any damage to the colony, and apparently gave inflated estimates of the number of breeding pairs to vindicate their activities. There is no doubt that this intense persecution, discussed bitterly in The Zoologist (Barrington 1890, Harvie-Brown 1890, Raeburn 1890, 1891, Traill 1890, Clarke 1892), resulted in a decrease in Great Skua numbers, from a peak around 1890 of some 40 breeding pairs (as determined accurately by Eagle Clarke (1892, 1894)) to only 17 pairs in 1899 (Holbourn MS). The influence of skin collectors was made worse over these years by the development of an egg collecting industry on Foula. Foula natives collected all first clutches and most second clutches each year and

sold these to egg dealers; a small number of third clutches were allowed to hatch, not so much to conserve the colony but because these eggs were deficient in pigment and undersized, so not of value to collectors (Holbourn 1938, Clarke 1892, 1894). While Foula was suffering this persecution, a similar destruction occurred at Ronas Hill, reducing this colony to three pairs in 1900 (Cramp, Bourne & Saunders 1974), but numbers on Hermaness increased, with occasional setbacks, as this colony was under the watch of a full time warden from 1891 onwards. In 1890 a fourth colony was established, with one pair breeding on Yell. This again appears to have been founded by a pair which may have deserted their natal area as a result of persecution and disturbance; Clarke (1894) mentioned that the breeding grounds on Foula were shifting from one part of the hills to another each year because the birds evidently "feel disturbed" by the persecution.

After 1900 egg and skin collecting ceased abruptly, although egg collecting for food replaced collecting of blown shells for export on Foula, and a small proportion of first clutches were removed each year. On Foula this practice still continues as a tradition, although nowadays only a dozen or so clutches are taken each year.

The relaxation of persecution has allowed the Foula colony to grow at an almost constant rate of 7% per annum since 1900, reaching 3000 pairs breeding in 1975. The Hermaness colony also increased after 1900, but at a slower rate (section 7), and a considerable number of new colonies have been established. Estimates of colony sizes from the literature are given for each British colony in appendices 2 to 27. These data are summarised in table 16, which also gives the number of colonies in each year, and the total British population of Great Skuas.

Table 16. Summary of the numbers of breeding pairs of Great Skuas in each British colony.

a) colonies founded before 1945.

Year	total colonies	number of pairs	Foula	Unst	R.Hill	Yell	Fetlar	Noss	Hascosay	Bressay	Hoy	Fair Isle	Mousa	Fitful Head
1774	2	10	7	3										
1780	1	8?	-	0										
1804	1/2	30	30									1??		
1821	1	30	30									0		
1828	2	-	-		1									
1831	3	-	-	3	-									
1832	3	-	-	3	5									
1837	2	-	-	-	0									
1850	2	36	6	30										
1860	2	-	3	-										
1861	2	9?	-	6										
1871	2	-	-	5										
1881	3	-	-	-	1									
1883	3	-	15	-	-									
1884	3	22?	16	5	-									
1885	3	-	-	6	-									
1886	3	-	-	6	-									
1887	3	-	(60)	8	-									
1888	3	-	-	9	4									
1889	3	-	(84)	9	-									
1890	4	66	40	9	16	1								
1891	4	-	(60)	9	-	-								
1892	4	-	-	9	-	-								
1895	4	-	-	7	-	-								
1897	4	-	-	23	-	-								

Table 16. a) Colonies founded before 1945 - Continued.

Year	total colonies	number of pairs	Foula	Unst	R.Hill	Yell	Fetlar	Noss	Hascosay	Bressay	Hoy	Fair Isle	Mousa	Fitful Head
1898	4	-	-	14	-	-								
1899	4	37?	17	-	-	-								
1900	5	-	-	-	3	-	1							
1905	5	70?	-	35	-	-	-							
1906	5	-	29	-	-	-	-							
1907	5	76?	-	42	-	-	-							
1910	6	-	-	-	-	-	-	2						
1913	8	-	-	-	-	-	-	-	4	1				
1914	9	-	-	-	-	-	-	-	-	1	1			
1917	9	-	-	-	-	-	-	-	-	-	1			
1921	10	-	-	-	-	-	-	-	-	-	4	1		
1922	10	-	-	100	3	-	-	12	-	-	3	-		
1923	10	-	-	-	-	2	-	14	-	-	2	-		
1924	10	-	-	-	-	-	-	15	-	-	-	-		
1925	12	-	-	90	-	-	-	-	-	-	2	-	2	2
1926	12	-	-	-	-	-	-	20	-	-	-	-	-	-
1928	12	-	-	-	-	-	-	30	-	-	-	-	3	-
1929	12	-	-	-	-	-	-	30	-	-	-	-	-	-
1930	12	-	-	-	-	-	-	-	-	-	-	3	-	-
1932	12	-	-	-	-	56	-	50	65	-	-	-	-	-
1933	12	-	-	-	-	-	-	-	-	-	8	-	-	-
1934	12	-	-	-	-	-	-	69	-	-	-	-	-	-
1936	12	-	-	-	-	-	-	-	-	-	-	3	-	-
1938	12	650?	300	120	-	-	-	80	-	-	-	-	-	-
1939	12	-	-	200	-	-	-	95	-	-	-	-	-	-

Table 16. a) Colonies founded before 1945 - Continued.

Year	total colonies	number of pairs	Foula	Unst	R.Hill	Yell	Fetlar	Noss	Hascosay	Bressay	Hoy	Fair Isle	Mousa	Fitful Head
1941	12	-	-	-	-	-	-	-	-	-	20	-	-	-
1943	12	-	-	-	-	-	-	-	-	-	-	1	-	-
1944	12	-	-	-	-	-	-	-	-	-	-	1	-	-
1945	13	-	-	-	-	-	-	-	-	-	-	-	-	-
1946	13	1030?	-	-	-	96	25	113	-	20	-	2	-	-
1948	14	-	400	-	-	-	-	-	35	-	-	4	-	3
1949	14	-	-	300	-	-	-	-	-	-	-	4	3	3
1950	17	-	-	300	20	-	15	-	-	-	-	6	3	-
1951	18	-	600	-	-	-	-	-	-	-	-	5	4	5
1952	19	-	-	-	28	-	25	165	75	-	-	10	-	5
1953	19	-	-	-	-	-	-	-	-	-	-	9	-	-
1954	19	-	-	-	-	-	-	-	-	-	-	8	-	-
1955	20	-	-	-	-	-	-	220	-	-	-	13	-	-
1956	21	-	500	-	-	-	-	-	-	-	-	17	-	-
1957	21	-	-	-	-	-	-	200	-	-	-	21	-	-
1958	22	1900?	1000	340	-	-	-	-	-	-	-	17	-	-
1959	22	-	-	-	-	-	-	-	-	-	-	19	-	-
1960	22	-	-	-	-	-	-	-	-	-	-	20	-	-
1961	23	-	-	-	-	-	-	-	-	-	70	20	-	-
1962	24	-	-	-	-	-	-	-	-	-	-	25	-	-
1963	24	-	900	-	-	-	-	-	-	-	-	31	-	-
1964	26	-	-	-	-	-	-	-	-	-	-	20	-	-
1965	26	-	-	300	-	-	-	-	-	-	-	12	-	-
1966	26	-	-	-	-	-	-	-	-	-	-	18	-	-
1967	26	-	-	-	-	-	-	-	-	-	-	12	-	-

Table 16. a) Colonies founded before 1945 - Continued.

Year	total colonies	number of pairs	Foula	Unst	R.Hill	Yell	Fetlar	Noss	Hascosay	Bressay	Hoy	Fair Isle	Mousa	Fitful Head
1968	26	-	-	-	-	-	-	-	-	-	-	10	-	-
1969	26	3200	1800	400	7	125	275	210	40	92	-	8	12	13
1970	26	-	-	-	-	-	-	-	-	-	-	8	-	-
1971	26	-	-	-	-	-	-	-	-	-	-	12	-	-
1972	26	-	-	-	-	-	-	200	50	-	-	13	20	-
1973	27	-	2500	-	-	-	-	230	-	-	-	-	-	-
1974	30	5000	2500	1078	100	120	237	242	55	175	400	17	9	50
1975	30	5700	3000	1100	-	257	280	250	-	160	503	-	-	-
1976	30	-	3000	-	-	-	-	255	-	-	462	-	-	-

Table 16. Summary of the numbers of breeding pairs of Great Skuas in each British colony.

b) Colonies founded after 1944.

Year	Lewis	Vaila	Urie Lingey	Papa West.	Dunnet Head	Tronda	Gluss Isle	Rousay	Eyn-hallow	Westray	St. Kilda	North Rona	Handa
1945	1												
1948	-	1											
1949	-	-											
1950	-	2	2	2	1								
1951	-	-	-	-	-	1							
1952	-	-	-	-	-	1	2						
1953	-	-	-	2	-	-	-						
1955	-	-	-	-	-	-	-	1					
1956	-	-	-	-	-	-	-	-	1				
1957	-	-	-	-	-	-	-	2	-				
1958	-	-	-	-	-	-	-	2	-	1			
1959	3	-	-	-	-	-	-	-	-	-			
1961	-	-	-	5	-	-	-	2	1	1			
1962	-	-	-	-	-	-	-	-	-	-	1		
1964	4	-	-	-	-	-	-	-	-	-	-	2	1
1965	-	-	-	-	-	-	-	-	-	-	-	2	1
1966	-	-	-	-	-	-	-	-	-	-	-	-	2
1967	-	-	-	-	-	-	-	-	-	-	-	-	3
1968	-	-	-	-	-	-	-	-	-	-	-	-	3
1969	10	6	2	6	-	0	1	-	-	-	8	-	3
1970	-	-	-	-	-		-	-	-	-	-	-	3
1971	-	-	-	-	-		-	-	-	-	10	-	3
1972	-	-	-	-	-		-	-	-	-	-	3	4
1973	-	-	-	-	-		-	-	-	-	-	-	5
1974	13	9	-	4	1		-	5	-	-	10	-	7

Table 16. Summary of the numbers of breeding pairs of Great Skuas in each British colony.

b) Colonies founded after 1944.

Other colonies not included in the table:

Colony	Year	Number breeding pairs
Sanday	1961	1
Eday	1969	1
	1974	1
Auskerry	1973	2
	1974	2
Birsay	1974	4
Stronsay	1974	3
Calf of Eday	1974	1

Faroe: quantitative

The first statistical reference to Great Skua populations in the Faroe islands is that of Svabo (1783), who stated that he was told that 6000 young were captured annually on the island of Skuø (Skuvoy) in the years around 1700. This statistic is impossible to accept, as Skuvoy is a very small island, with only 1.3 km^2 of cultivated land (on which Great Skuas would certainly not nest), 4 km^2 of pasture (on which Great Skuas would not normally nest in any numbers), and 1.5km^2 of rough moor (Joensen 1963). At present Great Skuas and Arctic Skuas occupy only 3 km^2 of the moor and marginal pasture land; if Great Skuas had occupied 5 km^2 in 1700, and had nested at the highest recorded breeding density for this species (600 nests km^{-2} in the Flick region of Foula in 1976) they would have had to raise an impossible average of 2.0 chicks per pair to produce the crop reputedly taken by man; yet at such a nesting density a breeding success of more than 1 chick per pair is highly improbable, and a greater nesting density could not be postulated as this would result in a further decrease in breeding success (see section 5). It seems probable that Svabo has confused the crop of another seabird with this species, as Suvoy has vast colonies of cliff-nesting species, and was an important island for fowling of Guillemots and other cliff-nesters (Williamson 1948). The alternative possibility is that 6000 is a gross exaggeration, and that a crop of Great Skua chicks was taken each year, but numbering only a few hundred individuals. There is no doubt however, that when Svabo visited the Faroes in 1782, only about 10 pairs of Great Skuas bred on Skuvoy (Svabo 1783), and no more than 45 breeding pairs have occupied this colony subsequently (Bayes, Dawson, Joensen & Potts 1964). In 1828 Graba (1830) found 50 pairs breeding at Sand on Sandø, but

only this one colony was visited. A complete census was not undertaken until 1872, when about 36 pairs were found altogether, scattered over eight colonies on seven islands (Fielden 1872); in 1897 these had been reduced by human persecution (principally skin collectors as in Britain) to only four pairs, inhabiting four different islands (Salomonsen 1935). As a result of this near-extinction of the species an Act of 18 December 1897 was introduced to protect the Great Skua from any form of persecution. It was successfully implemented, and numbers increased to about 71 breeding pairs in 1930 (Salomonsen 1931, 1935), occupying the same four colonies as the individual pairs which survived through 1897. After 1930 the increase continued, although the use of chicks and eggs as food resumed, and several colonies were subjected to illegal shooting of breeding adults to reduce their size, as the Faroese crofters dislike Great Skuas because of alleged lamb killing, their predation of other seabirds and their aggression towards humans. Documented changes in sizes of Faroe colonies since the initial quantitative description of Svabo (1783) are given in table 17. The increase after protection has been similar to that in Britain, but with a greater incidence of checks by crofters, so that the current population of the Faroes is rather small compared to that of Britain.

Status before quantitative data were available

It is not surprising that no counts of British Great Skua colonies were made before 1774; few quantitative data are available for earlier years for any seabirds, and indeed, the very existence of the Great Skua was unknown to a number of British ornithologists of the period. What is immediately surprising however, is the fact that there existed in Britain in 1774 only two colonies of Great Skuas,

Table 17. Estimates of the number of breeding pairs of Great Skuas in colonies in the Faeroes.

Year	Authority	Colony										
		Faroe Total	Svino	Vido	Bordo	Streymo	Vago	Sando	Skuvo	Stora Dimun	Stora Dimun	Sudero
1782	Svabo (1783)	-	-	-	-	-	-	-	10	-	-	-
1828	Graba (1830)	-	-	-	-	-	-	50	-	-	-	-
1872	Fielden (1872)	36	7	4/5	2/3	-	2/3	12/13	-	4	2/3	0
1897	Salomonsen (1935)	4	1	0	0	1	0	0	1	1	0	0
1930	Salomonsen (1935)	71	10	0	0	50	0	0	10	1	0	0
1942	Williamson (1945)	-	-	4/5	4/5	60/80	-	3	-	2	-	-
1946	Ferdinand (1947)	200	80/100	1	-	75/100	-	-	20	0	-	-
1948	Norrevang (1950)	-	400)	These estimates thought to be far too high by Williamson (1954)								
	Peterson (1950)	-	500)									
1951	Norrevang (1955)	1000 (too high; Williamson 1954)				-	6/7	-	-	-	-	-
1954	Bannerman (1963)	200	-	-	-	-	-	-	-	-	-	-
1961	Bayes et al. (1964)	530	200	14	15/18	235	1/2	10/20	40/45	2	0	2
1966	Gibbs & Mawby (1968)	-	-	-	-	102	0	22/23	20/25	-	-	-

with a total British population of only 10 pairs. The ease with which this species can be reduced by human persecution to the verge of extinction has already been shown, but in the late 18th century expeditions to collect bird skins were almost unknown, and less than a dozen specimens of Great Skuas were described from the period before 1800, of which all but two were obtained during autumn passage south through Europe. Furthermore, the Great Skua was not only protected from exploitation in Shetland by a severe fine, but was actively encouraged by Shetland natives who fed it in return for its defending lambs from the attacks of eagles. Only two hypotheses can explain this anomaly; either the Great Skua had been more numerous, but subject to severe persecution, or alternatively, it had only recently colonised Britain from elsewhere, and was establishing itself for the first time in Shetland with the aid of protection from the local inhabitants. Positive evidence to support the latter hypothesis is, by its nature, almost impossible to obtain, but there is evidence to suggest that the Great Skua was not a numerous species in Shetland at any time before 1774, making recent colonisation a probable answer.

The local Shetland name for the bird "Bonxie", is derived from the Old Norn "bonksi" or "bunksi", meaning a heap (often of clothes) or an untidy dumpy woman ("tyk og klumpet person" Jakobsen 1921) which aptly describes the species when on breeding territory, but not when flying. The name "Bonxie" is restricted to Shetland, and no local name for the species exists on Orkney or other Scottish islands, suggesting that it had never been found elsewhere in Britain. The similar word "bajnsi" is found in the 15th century Faeroese ballad "Fuglakvaedi", but this is thought to refer to the Great Black-backed Gull (Svabo 1783). The earliest use of the name "Bonxie" in the literature was by Low (1879) "here we find that remarkable bird the

Skua, called here Bonxie". Although published in 1879 Low wrote his article in 1774. Earlier British writers either did not know of this local name, or the name did not exist before this period.

Unfortunately, the classification of seabird species was a confused subject until the end of the 18th century. The names and descriptions supposed to relate to the Great Skua are numerous, but several were specimens of other species mistakenly referred to as Great Skuas by later authors or incorrectly identified as the same as earlier descriptions. An exhaustive list of the names given to specimens considered by the author or by later authors to be Great Skuas is given in table 18. The first description of a Great Skua was given by Clusius in 1605 from a specimen sent to him from the Faeroes by Hoier in 1604. Aldrovandi (1637) gives the second description of the species, but mistakenly equates it with the Catarracta of Aristotle (342 BC), which was clearly a Gannet in first year plumage "The catarractes lives near the sea; when it makes a dive it will keep under water for as long as it would take a man to walk a furlong"; the plumage is described as grey and brown all over. The third specimen of the Great Skua was described by Debes (1673), and was also collected from the Faeroes. Ray (1678) gives an accurate description of a Great Skua, the fourth in the literature, and calls it Catarracta after the name given by Aristotle and used by Aldrovandi. However, he also equates the species with the "Cornish Gannet", which is again clearly a first winter Gannet (Sula bassana) as he describes the method of capture used by Cornish fishermen which takes advantage of the feeding technique of the Gannet: A pilchard was fixed onto a block of wood which was weighted below and left floating at the surface of the sea. The birds then dived at the fish and dashed their brains out by impaling themselves on the block of wood.

Table 18. Classifications of specimens of Great Skuas, or of species mistakenly considered to be Great Skuas by later authors.

Name given	Authority	Work	Actual identity of specimen.
Catarracta	ARISTOTLE	Hist. Anim. IX 12 p615a (342 BC)	1st winter Gannet
Cepphus	ARISTOTLE	Hist. Anim. IX 12 p615 (342 BC)	Petrel sp.
Skua Hoieri	CLUSIUS	Exot. Decem Libri p 368-9 (1605)	
Catarractes omnis	ALDROVANDI	Ornithologiae III p 84 (1637)	
Cepphus	ALDROVANDI	Ornithologiae III p 93 (1637)	1st winter Arctic Skua
Skuen Debes	DEBES	Faeroae et Faer. Res. p 131 (1673)	
Catarracta	RAY	Orn. Will. p 348-9 (1678)	
Cornish Gannet	RAY	Orn. Will. p 348-9 (1678)	1st winter Gannet
Cataractes noster	SIBBALD	Scotia III. V (3) p 20 (1684)	
Larus fuscus	ALBIN	Nat. Hist. Birds 2 p 78 (1738-40)	1st winter Arctic Skua
Larus fuscus	BRISSON	Orn. vi p 165 (1760)	
Catharacta skua	BRUNNICH	Orn. Bor. p 32-38 (1764)	
Le Stercoraire raye	BRISSON	Orn. vi p 152 (1760)	1st winter Arctic Skua

Table 18. Classifications of specimens of Great Skuas, or of species mistakenly considered to be Great Skuas by later authors - Continued.

Name given	Authority	Work	Actual identity of specimen
Larus catarractes	LINNAEUS	Syst. Nat. i p 226 (1766)	
Larus keeask	LATHAM	Ind. Orn. ii p 818 (1790)	
Lestris catharractes	ILLIGER	Prodr. p 273 (1811)	
Catarracta fusca	LEACH	Syst. Cat. Mamm. & etc. Brit. Mus. p 40 (1816)	
Stercorarius catarrhactes	VIEILL.	N. Dict. d'Hist. Nat. xxxii p 154 (1819)	
Cataractes vulgaris	FLEM.	Brit. An. p 137 (1828)	
Stercorarius pomarinus	VIEILL.	Gal. des Ois. p 220 (1834)	
Lestris skua	JARDINE	Nat. Lib. 4, p 263-270 (1845)	
Megalestris catarrhactes	BONAP.	Cat. Parzud. p.11 (1856)	
Buphagus skua	COUES	Proc. Acad. Nat. Sci. Philad. p 125 (1863)	
Megalestris skua	RIDGEWAY	Nom. N. Amer. Birds p 53 (1881)	
Stercorarius skua	HARTERT	Die Vogel der pal. Fauna p 1756 (1916)	

Both Aldrovandi and Ray describe a bird which they give the name Cepphus. This name had been given by Aristotle to a species of small Petrel, but it is clear from the descriptions and figures in Aldrovandi and Ray that they were describing and naming specimens of the small skua species (Stercorarius parasiticus, pomarinus or longicaudus) in first winter plumage (when the three species are extremely similar). This mistake was compounded by several later authors who took these to be descriptions of the Great Skua. Further confusion arises, as Albin (1738-40) also describes a juvenile Arctic Skua, giving it the name Larus fuscus, or Brown Gull. The identity of the specimen is in no doubt as detailed measurements are given as well as an illustration. Unfortunately, the same name was used by Brisson (1760) to describe a specimen which was clearly a Great Skua. Brisson, in the same work, named a new genus, Stercoraire, into which he placed two "species"; Le Stercoraire raye, which was a first winter Arctic Skua, and Stercoraire a longue queue (longicaudus) which was probably an adult Arctic Skua. Subsequent descriptions were all assigned to the correct species, but many authors included these earlier mistakes in their lists of synonymy. Sibbald (1684) also describes a Great Skua, naming it Cataractes noster. This specimen was obviously observed on passage along the Scottish coast as its rapacious habit is also described, but it was clearly a species which was not well known to Sibbald, as he gives more space to it than to most other descriptions in this work. Brunnich (1760) gives the first detailed account of the species, giving a description, synonymy and summary of habits and status. He describes it as breeding in the Faeroes and Iceland, but does not include Shetland as a breeding place. When this omission is coupled with the fact that the Great Skua was not recorded in the list of British birds given by Merrett (1666), was not recorded by Brand (1701)

during his tour of Orkney and Shetland (although he gives an excellent description of the Arctic Skua (Berry & Davis 1970)), was not found by Sibbald during his visits to the Northern Isles (Sibbald 1711, 1739) although he knew of the species from a passage specimen (Sibbald 1684), and the British ornithologists Ray (1678) and Albin (1738-40) knew the species only from specimens obtained on passage, then it seems improbable that the Great Skua could have been a British breeding species at all before 1760. Pennant (1776) and subsequent authors give the breeding places of the Great Skua as Iceland, Faeroe, Shetland and, in some cases Norway. The last may be incorrect. There is no doubt that the Great Skua was known in Norway as an occasional passage migrant, but it probably did not breed there, and certainly did not breed there after 1850. It did however have a local name, in Norwegian "Kav-Oern" (Pennant 1776, Brunnich 1760), which suggests that it may have bred there for a period in the 18th century, but evidence in favour of this possibility is very weak.

There is stronger evidence to suggest that the Great Skua did not breed in Shetland during the Bronze Age or the Viking periods (which cover the years up to 1000 AD). Although seabirds were important in the diet of the inhabitants of Jarlshof in Shetland (Hamilton 1953, 1956) the Great Skua was not among the many species found in the refuse middens (table 19). Nor have bones of the Great Skua been found at any other middens which have been examined (table 19). As this species is very easily harvested, adults were caught at sea by Belgian fishermen using baited lines, and chicks were harvested both in Iceland and the Faeroes (Gudmundsson 1954, Salomonsen 1935), so it seems unlikely that it would not have been exploited if it had been present in Shetland in these periods. It seems probable that the Great Skua colonised Britain for the first time only a few years before 1774 when Low (1879) visited the two colonies in Foula and Unst.

Table 19. Identified seabird bones associated with late Pleistocene and prehistoric human cultures in northern Scotland. The lists on which this table is based are published in the Proceedings of the Society of Antiquaries of Scotland from 1900 to 1976, Hamilton (1956), MacKie (1974) or are held in the Dept. of Natural History, The Royal Scottish Museum. Three bones had originally been identified as Great Skua, but on re-examination by Dr. A.S. Clarke, these were found to be of other species.

a) Bones listed as Great Skua

Archaeological site	Bone reference No.	Actual identity
Aikerness Broch	1935.104.38	Brent Goose
Priest Island	1940.9.38	Herring Gull
Midhowe Broch, Rousay	1941.13.38	Herring Gull

b) Frequency of occurrence of bones of seabird species at 18 sites (corrected)

Species	Frequency	Species	Frequency
Cormorant	15	Red-throated Diver	2
Gannet	14	Eider	2
Great Auk	9	Great Northern Diver	1
Guillemot	8	Arctic Skua	1
Puffin	8	Storm Petrel	1
Shag	8	Black-headed Gull	1
Razorbill	6	Kittiwake	1
Little Auk	6	Common Gull	1
Great Black-backed Gull	6		
Herring Gull	4	Great Skua	0

The status of the Great Skua in Faroe before 1780 is confused. It was clearly a breeding summer visitor in 1604 when Hoier collected the first described specimen of the species (Clusius 1605), as Hoier wrote of it "it produces young carelessly on open ground from olive eggs, bigger than but similar to those of ducks, which are marked by thin black spots. It feeds on fish but also takes food from every kind of bird indiscriminantly" (translated from Clusius 1605). Debes (1673), who visited the Faroes in 1672, also records the Great Skua as a breeding species "in defending its eggs and chicks, in flying over it flies at their (intruders) heads and beats these with its wings; hence the native inhabitants, to whom the ferocity of this bird is well known, hold a knife with the sharp edge uppermost above their head, on which the bird is frequently transfixed". The Faroese ballad "Fuglakvaedi", written in the 15th century, names 38 species of bird, including "skuvur", which seems to be a clear reference to the Great Skua (Salomonsen 1935) but I have not seen a copy of this ballad, so the breeding status of the Great Skua at that time is not certain.

While Svabo (1783) clearly exaggerated the size of the Great Skua population of the Faroes in the early 18th century, it is generally accepted that the species was common throughout the islands up to the middle of that century, while the decline of the species over this period is attributed to overexploitation of chicks as a food source by the Faroese (Salomonsen 1935). Such uncontrolled exploitation would be in stark contrast to the careful management of other seabird populations practiced by Faroese fowlers (Fisher & Lockley 1954). A further anomaly is the omission of the Great Skua from the bill tax. This tax required every man from his 15th to

his 50th year to deliver a Raven's bill, or two bills of Hooded Crow, Great Black-backed Gull, Herring Gull or Lesser Black-backed Gull each year. Delivery of a Sea Eagle bill exempted the bearer from the tax for the rest of his life. The Great Skua did not join this list of vermin until 1800, when one Great Skua bill became equivalent to one gull or crow bill, and this tax was enforced until 1881 (Salomonsen 1935). By 1800, the Great Skua in the Faroes had, according to Svabo and Salomonsen, been reduced through collection of young for food, to only a small proportion of the numbers of earlier decades, yet it became a vermin species only after this reduction. It is difficult to understand why it was not considered to be vermin when more numerous, and it is difficult to believe that cropping of chicks without persecution of adults would lead to a drastic population reduction, as it is difficult to find much more than half of the chicks without considerable time and effort (as shown by Brathay's capture-recapture studies (section 1)); effort which the Faroese would have expended in more profitable activities. However, Svabo (1783) suggests that the Great Skua was included in the bill tax vermin list in the 17th century, although he was not certain whether it was still on the list after 1746. If so, persecution of adults may have caused the supposed decline. A detailed examination of the Fuglakvaedi and Faroese records of bills collected in taxation, which is outside the scope of this thesis, would be required to elucidate this situation.

Iceland, for obvious reasons, has the least detailed documentation of Great Skua status. No quantitative data are available before the subjective estimates of Gudmundsson (1954), and few publications on the birds of Iceland exist. One of the earlier, and detailed, accounts was given by Jon Gudmundsson, who lived between 1574 and 1650, and who is quoted by Timmerman (1938) "Die grosse Raubmöwe brütet hierzulande".

Clearly the Great Skua was breeding in Iceland in the early 17th century. However, an appendix to the Snorra Edda, which was compiled in the 12th century and includes names of 117 species of bird, includes the name of only one species of skua, "skufr", (Snorra Sturlason; reprinted by Jonsson 1907). This name was apparently used to describe the Arctic Skua (Zoega 1942), as well as the Great Skua (Fritzner 1896), although in modern Icelandic the Arctic Skua is called "kjoi" (Sigurdsson 1970) and this name was used indiscriminantly for Long-tailed and Pomarine Skuas as well as Arctic Skuas (Slater 1901). The name, also given as "kjogvi" (Williamson 1946), "kjeui" (Salomonsen 1935), "tjegvi" (Fielden 1972) or "tyovi" (Landt 1800), means thief (Williamson 1946). This name, although used in the 15th century Faroese "Fuglakvaedi" (Salomonsen 1935) was not included in the Snorra Edda list, although it seems reasonable to assume that the Arctic Skua was a common breeding species in Iceland at that time. However, if skufr is not to be taken to have meant Arctic Skua it is difficult to see why the name was transferred to the Great Skua and then the Arctic Skua name altered, although such changes are not infrequent in ornithological history (our Herring Gull and Lesser Black-backed Gull used to be called Silver Gull and Herring Gull respectively (Latham 1824) and Larus fuscus, now describing the Lesser Black-backed Gull, used to refer to the Great Skua (Brisson 1760) and earlier to the Arctic Skua in first winter plumage (Albin 1740)). Only in Shetland does the Arctic Skua have a name similar to skufr. Here it is called "skooi", which is supposed to be derived from the completely different word "skoot", meaning excrement, upon which Arctic Skuas were considered to feed (Newton 1896, Venables & Venables 1955). The name skufr means a tassel, or headscarf, (de Vries 1961), and is also given as "skumur" or "skumr" (Pennant 1776), "skue", "skugvur", "skuvur" or "skuir" in the Faroes, and was the origin of the word "skua", adapted from the Faroese by

Hoier (Murray 1888 vol IX p 156). It is hard to see why the Great Skua should be described as a bird with a tassel or a headscarf, although the light phase Arctic Skua could fit such a description. The presence of only one name, skufr, in the Snorra Edda, does suggest that only one of the two species of skua was then to be found in Iceland, as such obvious birds are unlikely to be left out of such a long list. Given these ambiguities of nomenclature, it seems more likely that the Great Skua was absent rather than the alternative. This raises the possibility that the Great Skua may not have colonised the North Atlantic until after 1200 AD, although it was established by 1500 AD. Some support is given to this possibility by the very close similarity of the North Atlantic birds, in measurements and plumage, with the race of Brown Skua found on Tristan da Cuhna and Gough Island (Devillers in press, in litt.), suggesting that North Atlantic populations were recently derived from this stock.

One implication of this history is that Great Skuas are relatively new members of North Atlantic seabird communities, and therefore not "coadapted" members (Cody 1973). The Great Skua is now more numerous than it ever has been in the past, so it is not simply returning to an equilibrium population size after relaxation of 19th century persecution, as might appear to be the case by analogy with the Gannet (Fisher & Vevers 1943, 1944) and the Kittiwake (Coulson 1963, 1974). A consequence of this situation is that other seabird species may not be adapted to withstand harmful effects of Great Skuas and might decline in numbers in areas where Great Skua populations are increasing.

SECTION 3

MIGRATIONS AND COLONY OCCUPANCY

Introduction

Great Skua migration cannot be adequately studied by direct observations from headlands, as this species tends to remain too far offshore to be counted on passage, except during adverse weather conditions. Sight records cannot usually be classified into adults and juveniles as age identification is difficult in the field. Furthermore, Salomonsen (1976) has pointed out that a number of North Atlantic records must refer to South Polar Skuas C. maccormicki, which may spend the austral winter as far north as Greenland and Japan (Devillers in press). The other southern species, the Brown Skua C. skua lönbergi has also been recorded in the North Atlantic, north of the equator (Hudson 1968), while the North Atlantic race C. skua skua has been recorded south of the equator, on the Brazilian coast, so their nonbreeding distributions also overlap to an uncertain extent.

These problems require that migrations are studied using data from ringing programmes. These data are susceptible to a number of serious biases. In many long-lived species, rings become worn and illegible, or fall off before the bird dies, so fewer recoveries of older birds are obtained than would be expected (Coulson & White 1955, 1957, Harris 1964). The rate of ring wear may vary between similar species and between sexes of the same species (Coulson 1976). During the past 14 years or so, monel (nickel-copper alloy) has been used by the BTO in an attempt to improve the life of rings, particularly on

seabirds, as the aluminium rings used up to the early 1960's wore extremely rapidly (Poulding 1954).

Only a small proportion of ringed birds are found and reported to the BTO. The chances of a bird being reported are higher if it dies in an urban area or is caught in fishing nets, and negligible if it dies on the ocean, so recovery data will represent other factors as well as distribution or mortality rate, and these other factors may obscure or even reverse trends in the data caused by the factors to be studied. For example, recoveries of ringed Kittiwakes tend to occur in the summer, which is when people visit beaches, but mortality, determined by disappearance of colour marked individuals, was found to be greatest during the winter (Coulson & Wooler 1976).

An analysis of the 119 recoveries of Great Skuas available in 1965 was made by Thomson (1966). The more numerous data now available allow a more detailed examination of the movements of the Great Skua, taking the various biases into account.

Ring wear

Six sequences of size H BTO rings (monel) were unpacked, and each ring weighed on a Mettler H16 balance to an accuracy of 0.0001 g. The sequences used were 420132 to 420150, HW 05412 to HW 05440, HW 46951 to HW 46980, HW 47221 to HW 47250, HW 52051 to HW 52080 and HW 52951 to HW 52980. These were chosen because they were conveniently at hand, and are assumed to be representative of size H monel rings of all series.

A runs test above and below the median indicated that the weight of each ring, with respect to the median, is effectively independent of the weight of rings adjacent in sequence; independence was also indicated by a runs up and down test (table 20).

Table 20. Runs tests to determine whether ring weights show any autocorrelation within series.

Sample number	number of rings weighed	runs above and below median	probability by chance	runs up and down	probability by chance
1	19	10	> 0.05, ns	13	> 0.05, ns
2	29	13	> 0.05, ns	18	> 0.05, ns
3	30	13	> 0.05, ns	14	> 0.05, ns
4	30	17	> 0.05, ns	23	> 0.05, ns
5	30	15	> 0.05, ns	21	> 0.05, ns
6	30	8	= 0.01	14	> 0.05, ns

Weights may therefore be assumed to be randomly distributed within sequences, allowing further statistical examination. The F max test of homoscedasticity gives $s^2max/s^2min = 2.80$, $p > 0.05$, ns. The more powerful Bartlett's test for homogeneity of variances also indicates that sequences are homoscedastic (m/c = 7.62, df = 5, ns). Testing for heterogeneity of sample means indicates that there are significant differences between sequences (table 21, $F_{5,162} = 2.984$, $p < 0.05$).

Table 21. Anova table testing for variation between sequences in the weights of size H monel rings.

Source of variation	df	sum of squares	mean square	F
among sequences	5	0.03323	0.006646	
within sequences	162	0.36080	0.002227	2.984
Total	167	0.39403		

That the extent of variation between sequences is small is shown by the coefficient of intraclass correlation of 0.066, indicating that only 6.6 % of the variance in ring weights is due to heterogeneity of sequence means. It therefore seems reasonable for the purposes of ring wear studies to ignore the small differences between sequences and consider size H monel ring sequences to be homogeneous in mean weight and variance of weights. Frequency distributions of ring weights indicate that each sequence has an approximately normal

distribution of weights. For the 168 rings of all six sequences the mean weight is 3.2996, with a standard deviation of 0.0486. The normal distribution with these parameters is an acceptably close fit to the observed distribution for all sequences ($X^2_8 = 19.0$, $p = 0.02$). For the purpose of quantifying ring wear it is sufficient to assume unused ring weights to be normally distributed with mean 3.300 g and standard deviation 0.049 g.

Rings were removed from a total of 48 ringed Great Skuas which were found dead or retrapped on Foula between 1972 and 1976. These rings were weighed to the nearest 0.0001 g, and the regression of ring weight on age of bird was calculated to be;

$$\text{weight} = 3.266 - 0.00498 \text{ age (in years)}$$

for which the correlation coefficient is not statistically significant ($r = -0.196$, $df = 46$, ns) suggesting that negligible ring wear occurs in the first 13 years of a Great Skua's life. Comparing the rate of wear of Great Skua rings with rates determined for Herring Gulls and Lesser Black-backed Gulls (Coulson 1976) shows that rings on Great Skuas will last considerably longer than those on gulls (table 22).

Table 22. Rates of ring wear by Great Skuas (this study) and by two species of gull (Coulson 1976); all birds ringed as pulli.

Species	sample size	ring weight loss (g yr -1)	standard error of rate	years to loss of half ring weight.
Great Skua	48	0.0050	0.0037	330
Lesser Black-backed Gull	48	0.0639	0.0068	23
Herring Gull	769	0.1120	0.0012	13

It seems reasonable to assume that every monel ring put onto a Great Skua will remain on the skua and legible until the bird dies, in spite of the longevity of the species, so no bias will arise as a result of monel ring wear. Aluminium rings are no longer available for studies of wear, but the effect of loss of alumium rings can be seen in the recovery rates of Great Skuas ringed before 1961 (all with aluminium rings) compared with recoveries of monel-ringed birds, ringed in or after 1965, for which no ring loss will have occurred. The percentage of Great Skuas ringed as chicks with aluminium rings and recovered in their first or second year is higher than the percentage recovered from chicks ringed with monel rings, so there is no sign of loss of aluminium rings in the first two years of life. Only eight of 2500 pulli (0.32%) ringed before 1961 were recovered aged two or older, while 150 of 13000 (1.15%) ringed between 1965 and 1972 had already been recovered aged at least 2 years by 31 December 1974, although more of these birds are still alive and will be recovered in the future. The difference is highly significant ($t = 3.77$, $p < 0.01$), and indicates that considerable loss of aluminium rings starts to occur after the second year of wear. No aluminium ring is known to have lasted for more than five years on a Great Skua.

Ringing data available

Nearly 24 000 Great Skuas have been ringed in Britain up to the end of 1974. Of these, only 0.2% were ringed when adult, and none of these individuals have been recovered, so all recoveries are of birds of known age and origin. Up to 31 December 1974 a total of 492 ringed Great Skuas had been recovered after fledging and reported to the BTO. Another nine were retrapped during the breeding season and reported. The number of Great Skua chicks ringed each year is recorded, but the

number ringed in each colony in each year has been calculated only for Foula. There are no significant differences between recoveries of Foula or other Great Skuas so it is assumed that all Shetland colonies can be considered as a homogeneous unit. The number of chicks ringed and recovered in each year is given in table 23. The number of recoveries from each colony up to 31 December 1974 is given in table 24. Great Skuas ringed on Foula which were recovered and reported to the BTO after 31 December 1974 but before 1 May 1977 are also included in the analysis where these add to the conclusions drawn from the earlier data.

Causes of death

The cause of death of each bird is recorded on the recovery slip, and the following categories were distinguished; "found dead", "found exhausted or injured", "killed", "caught in net or on hook" or "unreported". Very few recoveries did not have the cause of death clearly recorded so the few "unreported" individuals have been excluded from the analysis. The frequency of each recovery category varies geographically, annually and with age of bird. There is no evidence to suggest changes in the causes of death over the period 1923 to 1974, other than annual fluctuations which will be examined later. To examine the relative importance of mortality factors in different age groups and geographical regions, indices similar to those used by Coulson & Brazendale (1968) have been employed. These express "killing intensity" and "catching intensity" independently of each other so that differences in one do not influence the value of the other.

Table 23. Numbers of Great Skua chicks ringed in each calendar year and the numbers recovered from each cohort, and in each calendar year.

Year	Total ringed:			Total recovered:	
	Foula	others	total	of cohort	in that year
1923-38	0	130	130	3	3
1939	0	373	373	15	13
1940-56	30	649	679	5	6
1957	108	47	155	0	0
1958	110	169	279	5	3
1959	199	235	434	10	7
1960	358	70	428	10	5
1961	329	173	502	22	11
1962	797	283	1080	31	11
1963	822	175	997	44	42
1964	317	260	577	21	13
1965	975	38	1013	44	25
1966	1264	133	1397	49	20
1967	1047	157	1204	31	27
1968	636	457	1093	30	22
1969	1527	773	2300	79	47
1970	1155	651	1806	30	42
1971	1577	153	1730	21	43
1972	1726	854	2580	23	58
1973	1354	654	2008	11	47
1974	1666	836	2502	8	47
TOTAL	15 997	7 270	23 267	492	492

Table 24. Number of ringed Great Skuas recovered from each colony.

Colony	number recovered
Foula	367
Hermaness	73
Noss	26
Bressay	7
Fair Isle	5
Fetlar	4
Hoy	4
Mousa	2
Hascosay	1
Libbers Hill	1
Lungawater	1
Saxavord	1
TOTAL	492

Killing intensity is expressed as:

$$\frac{\text{Number killed}}{\text{Number killed + number found dead + number exhausted}}$$

Catching intensity is expressed as:

$$\frac{\text{Number caught}}{\text{Number caught + number found dead + number exhausted}}$$

Exhaustion intensity is expressed as:

$$\frac{\text{Number exhausted}}{\text{Number found dead + number exhausted}}$$

Using these indices, no significant differences could be detected in the causes of death of age groups of Great Skuas more than one year old, but the relative importance of each factor differs between first year and older birds. In all geographical regions, first year birds* are more susceptible to being killed than older birds (paired $t = 2.75$, $df = 6$, $p < 0.05$) and are more likely to be found exhausted (paired $t = 4.13$, $df = 6$, $p < 0.01$). A similar greater susceptibility of young birds to being shot has been shown from ringing data by Lloyd (1974) and Birkhead (1974) for Razorbill and Guillemot, although these authors failed to take into account differences in the dispersion of different age groups which, in auks, result in more first year birds reaching areas of high shooting intensity. A bias of shooting selecting young birds has been shown by Murton (1961) for the Wood-pigeon, and is probably a normal phenomenon. Without eliminating

geographical effects, no difference in killing intensity between young and older birds would have been apparent, as a large proportion of birds killed were killed in the Faroes or Greenland, areas which are not visited by first year birds. The greater mortality of first year birds as a result of exhaustion is in part due to their greater susceptibility in "wreck" years (Thomson 1966). The inexperience of fledglings in flying and feeding, together with their incomplete physical development, results in larger numbers of this age group being driven onto or over the coast of Europe, some being recovered on the point of death many miles inland. Although the chances of becoming caught in nets appear equal for first year and older birds (paired $t = 0.34$, $df = 6$, ns), the proportion of older birds caught in nets in Britain is significantly higher than the proportion of first year birds caught ($t = 2.05$, $df = 55$, $p < 0.05$) although other geographical regions all suggest a slightly higher susceptibility of first year birds. The difference in Britain may be behavioural. Older birds move away from the breeding colonies more slowly than first year birds during the autumn, and so must spend more time feeding around the coast of Britain, making themselves more liable to becoming tangled in nets.

Because the chances of a first year bird being reported killed or exhausted are higher than those for an older bird, analysis of geographical differences in mortality factors has to be done separately for first year and for older birds. Heterogeneity tests using X^2 divide recoveries into several geographical groups of areas which are homogeneous in proportions of recovery types, but differ significantly from each other (table 25).

Geographical groupings can be made by comparing values of killing, catching and exhaustion indices. The results are essentially the same,

Table 25. Causes of death of Great Skuas recovered in different regions; areas are grouped into homogeneous units. All recoveries except those for which no cause of death was reported are included if reported to the BTO before 31 December 1974. 0 = first year, 1 = older.

Area	age when recovered	recoveries	cause of death: found dead	exhausted	caught	killed
Shetland/Orkney	0	7	5	2	0	0
	1	87	72	5	7	3
Britain (rest)	0	33	18	12	1	2
	1	27	17	4	5	1
Scandinavia/Belgium	0	28	9	6	1	12
	1	16	11	1	1	3
Netherlands/Germany	0	36	24	9	0	3
	1	14	12	2	0	0
France	0	50	23	14	0	13
	1	34	24	4	0	6
Spain/Portugal	0	48	8	5	22	13
	1	35	8	6	9	12
Greenland/Faroes	0	0	-	-	-	-
	1	30	2	0	4	24
"all other areas"	0	22	4	7	4	7
	1	14	5	2	4	3
Totals	0	224	91	55	28	50
	1	257	151	24	30	52

but the use of X^2 is less robust than the use of a distance measure based on index values. The latter, used in numerical taxonomy (Sokal & Sneath 1963) is defined as;

$$d^2_{a,b} = (x_a - x_b)^2 + (y_a - y_b)^2 + (z_a - z_b)^2$$

where, in this study, x = killing intensity, y = catching intensity, z = exhaustion intensity, and $d_{a,b}$ is a measure of distance (dissimilarity) between mortality factors of two geographical regions. Unlike X^2, the value of $d_{a,b}$ is independent of sample size. The relationship between mortality factors in different regions can be shown by constructing a dendrogram to link regions according to their distance values; these are shown in figures 6 and 7. The percentage of recoveries in each cause of death category is shown below each dendrogram to indicate the relative importance of each in determining the relationships. First year birds fall into three similar categories; Shetland, Orkney, Netherlands, Germany and Britain form one category, France, Scandinavia and Belgium a second, and Spain, Portugal and "other areas" a third. Older birds fall into three slightly different groupings; Greenland and Faroe form one group, Spain, Portugal and "other areas" the second, Shetland, Orkney, Britain, Netherlands, Germany, France, Scandinavia and Belgium the third. The particularly high proportion of birds killed in Greenland and Faroe, and high proportion caught in nets in Spain and Portugal, will overemphasise the occurrence of Great Skuas in these regions, as the chances of a ringed bird being reported are very much higher with these causes of death than for individuals which die not in association with man.

Wrecks of seabirds, particularly of the more pelagic species, have been periodically recorded for centuries. They are usually

Figure 6. Causes of death reported for British ringed Great Skuas less than one year old. The upper figure is a dendrogram which shows the "distances" $D_{a,b}$ between geographical regions in the proportions of each cause of death. Below the dendrogram the percentages of recoveries reported as found dead, exhausted, caught (usually in fishing net) or deliberately killed, are shown for each region.

Regions are: a. Shetland and Orkney

b. Netherlands and Germany

c. rest of Britain and Ireland

d. France

e. Norway, Denmark and Belgium

f. Other areas

g. Spain and Portugal.

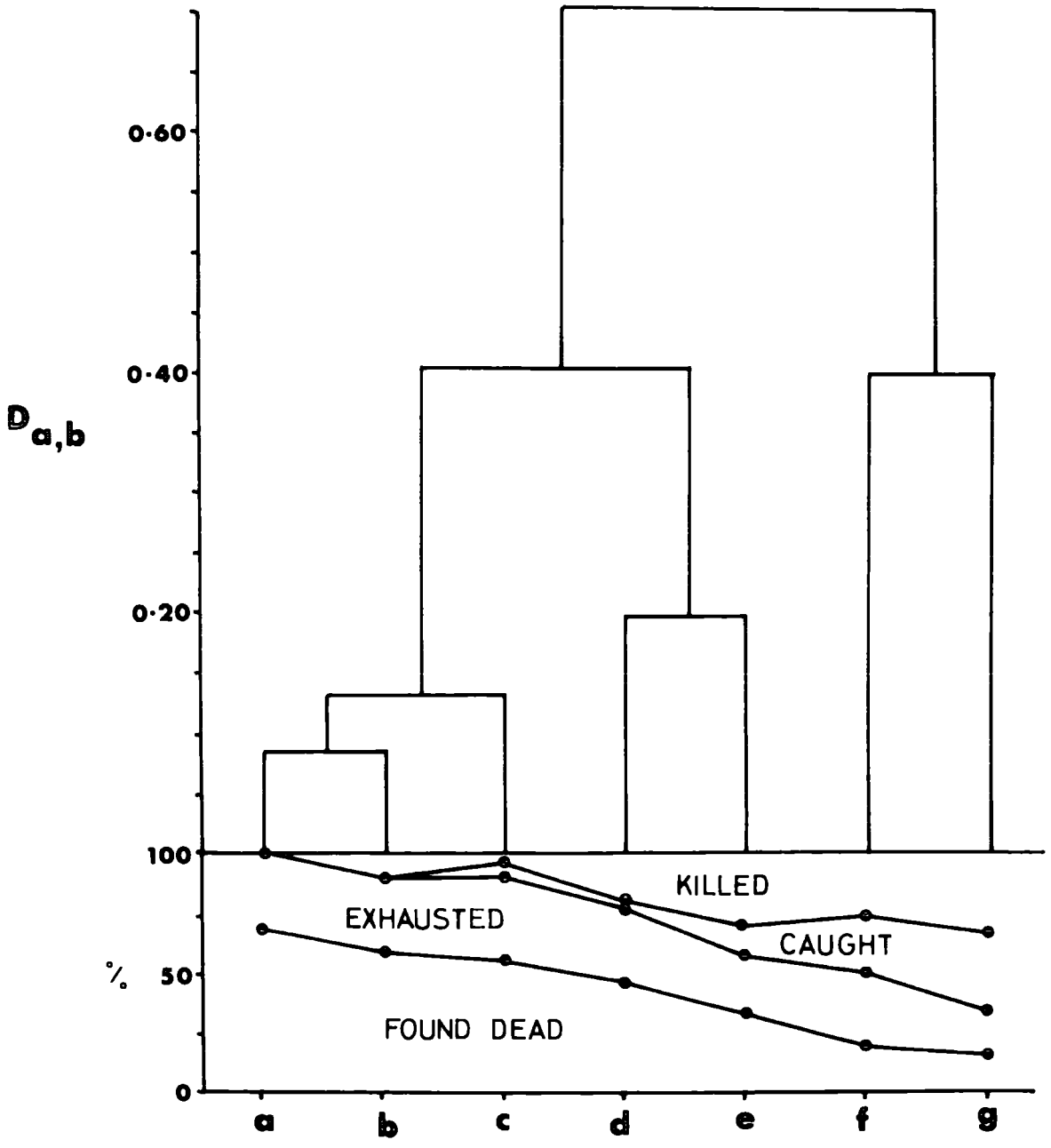
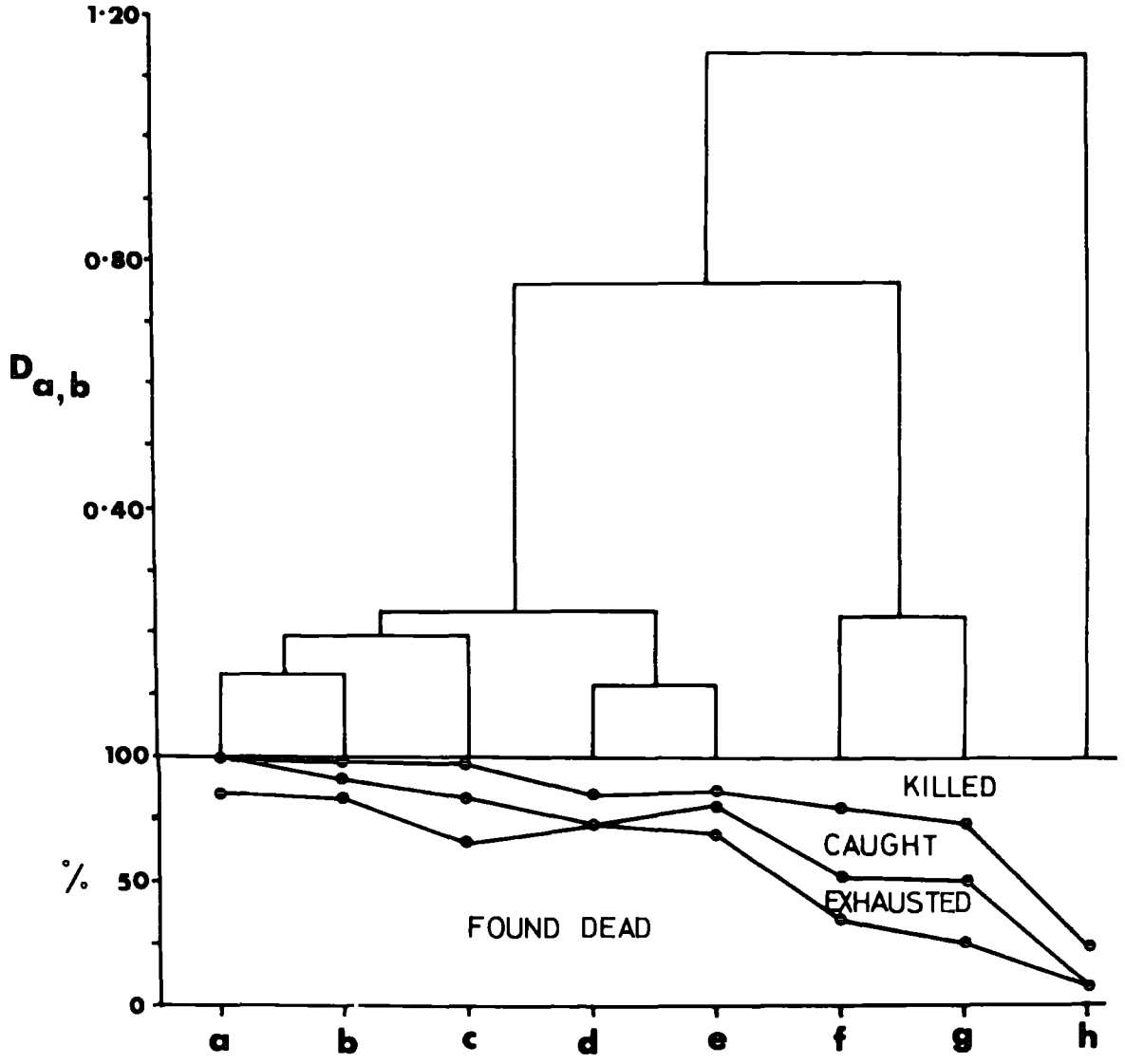

$D_{a,b}$
0·60
0·40
0·20
100
50
0
%
KILLED
EXHAUSTED
CAUGHT
FOUND DEAD
a
b
c
d
e
f
g

Figure 7. Causes of death reported for British ringed Great Skuas more than one year old. The upper figure is a dendrogram which shows "distances" $D_{a,b}$ between geographical regions in the proportions of each cause of death. Below the dendrogram the percentages of recoveries reported as found dead, exhausted, caught (usually in fishing net) or deliberately killed, are shown for each region.

Regions are:
a. Netherlands and Germany
b. Shetland and Orkney
c. Rest of Britain and Ireland
d. France
e. Norway, Denmark and Belgium
f. Other areas
g. Spain and Portugal
h. Greenland and Faroes


1·20
0·80
$D_{a,b}$
0·40
100
%
50
0
KILLED
CAUGHT
EXHAUSTED
FOUND DEAD
a
b
c
d
e
f
g
h

associated with particular weather conditions at a certain time of year. Tuck (1960) correlated wrecks of auks with onshore gales, suggesting that large numbers of pelagic birds may, under these conditions, be caught with little searoom for manoevring and may be carried inland as a result. Thomson (1966) associated the 1939 and 1963 Great Skua wrecks with Northerly and North-westerly gales during autumn movement into the North Sea, resulting in numbers of Great Skuas being driven into continental Europe. Wrecks would be expected to result in a high proportion of recoveries of exhausted individuals, and also of a high total recovery rate in that autumn. The variation in the recovery rate of first year Great Skuas is shown in table 26. It is this age group that is most severely affected by adverse weather conditions.

The recovery rate over the period 1923 to 1966 is 110/7000 (1.57 %), significantly higher than that for the period 1967 to 1974 which was 117/15000 (0.78 %) ($t = 5.11$, $p < 0.001$). This change cannot be ascribed to changes in killing or catching pressures, as neither index has changed significantly over the period, and while killing intensity appears to have declined slightly, catching intensity has increased, so these trends will tend to cancel each other. There is evidence of a change in the geographical distribution of recoveries. Since 1967 these have tended to be of a more southwesterly nature than those of earlier years. Division of Europe through the borders between Belgium and France, and the classification of recoveries of first year birds as "northeast" or "southwest" on the basis of falling above or below this line gives the contingency table below (table 27).

These data suggest that the dispersal of Great Skua fledglings has become more pelagic in recent years, with fewer individuals being recovered in North Sea areas ($X^2_1 = 4.06$, $p < 0.05$). This conclusion

Table 26. Recovery rates of first year Great Skuas ringed in all colonies.

Year	number ringed	number recovered	percentage recovered
1938	130	3	2.31
1939	373	14	3.75
1940-56	679	2	0.29
1957	155	0	0.00
1958	279	2	0.72
1959	434	6	1.38
1960	428	4	0.93
1961	502	8	1.59
1962	1080	12	1.11
1963	997	27	2.71
1964	577	5	0.87
1965	1013	12	1.18
1966	1397	15	1.07
1967	1204	9	0.75
1968	1093	7	0.64
1969	2300	38	1.65
1970	1806	14	0.77
1971	1730	14	0.81
1972	2580	17	0.66
1973	2008	10	0.50
1974	2502	8	0.32

is strengthened by the occurrence in recent years of recoveries in Brazil, Cape Verde Islands, Canaries and North Africa, areas from which ringing recoveries of Great Skuas were unknown before the mid 1960's. Thomson (1966) showed that in wreck years recoveries tend to fall mainly in northeastern areas, particularly Belgium, so the difference may reflect less severe autumn weather in recent years. The fact that 27% of first year recoveries since 1966 were of exhausted birds, while only 20% of recoveries prior to 1967 were in this category suggests that the autumn weather conditions have probably not become any more favourable since 1966. In the wreck years 1939 and 1969 a significantly higher proportion of first year recoveries were of exhausted birds, although the difference in 1963 was not statistically significant. It seems reasonable to expect gales which force numbers of birds inland to result in a greater recovery of exhausted individuals, so the implication, that wrecks have not become less frequent and typical autumn conditions no less severe, supports the suggestion of a change to a more pelagic dispersal pattern. This change would also

Table 27. Geographical distribution of recoveries of first year Great Skuas in years before and after 1967. (Expected values if no heterogeneity between time periods are given in parentheses).

Period	Northeast	Southwest	total
before 1967	46 (38.4)	58 (65.6)	104
after 1966	47 (54.6)	101 (93.4)	148

be expected to result in a decrease in the recovery rate of first year birds, as observed, as the North Sea coasts are far more densely populated than the west coasts of Scotland and Ireland, or the Atlantic Ocean.

The mean recovery rate of first year birds* before 1967 is 1.38 (sd = 0.48). For the years after 1966 the mean recovery rate is 0.76 (sd = 0.34). If a wreck is defined as any year yielding a recovery rate of first year birds more than two standard deviations greater than the mean, or above 2.34 % before 1967 and 1.44 after 1966, then wrecks occurred in 1939, 1963 and 1969. Examination of the recovery data from cohorts ringed on Foula since 1963 (ie with monel rings) indicates that in years of high first year mortality there is also a tendency for high mortality of older birds. The correlation coefficient between first year mortality rate and the mortality rate of second year birds in the same year (+0.59, $t = 2.31$, $df = 8$, $p < 0.05$) is the only one to be statistically signigicant, but mortality rates of third year birds are also positively correlated with first year mortality (+ 0.50, $t = 2.13$, $df = 8$, $p < 0.10$), as are mortality rates of fourth year birds (+ 0.52, $t = 1.93$, $df = 7$, $p = 0.10$), suggesting that all age groups suffer to some extent in years of bad weather conditions.

As well as the correlation between mortality rates of different age groups in each year, there is a correlation between recovery rates of a particular cohort in successive years. Thus a cohort which suffers high mortality in its first year also tends to suffer high mortality in its second year. It would appear that first year birds which are subjected to stress are unable to recover completely before the stresses of their second autumn. The correlation coefficient between first year and second year mortality of the same cohort for

years 1962 to 1973 is + 0.59, $t = 2.3$, $df = 10$, $p < 0.05$. There is a positive, but small and not statistically significant, correlation between first year and third year mortality of the same cohort, but many more years of data would be required to determine how long the effect of a bad first autumn continues to affect survival.

These ringing data, and observations of colour ringed Great Skuas recruiting into the Foula population (see below), indicate that different cohorts suffer very variable degrees of pre-breeding mortality. A striking example is the shortage of 1969 colour-ringed birds (a wreck year) in Foula clubs and territories compared with 1968 and 1970 cohorts.

Movements of different age groups

The analysis of recoveries of a pelagic species such as the Great Skua is complicated both by the atypical nature of most recoveries, and by the differential susceptibility of different age groups to mortality factors and differences in mortality factors in different geographical regions. However, comparisons of the recoveries of birds of different ages and at different seasons show marked patterns of movement over the range of the species, which extends to Arctic Norway, Northwest Greenland, Brazil, Guyana and Malta. Recoveries of birds in their first year fall into five geographical categories:

1. "Home waters" (Shetland, Orkney, Scotland, England, Ireland)
2. "Wreck areas" (eg USSR, Poland, Austria)
3. "East North Sea" (Denmark, Germany, Netherlands, Belgium)
4. "East Atlantic" (France, Spain, Portugal)
5. "South of Europe (Mediterranean, Morocco, Canaries, Cape Verde Islands, Guyana, Brazil)

Thomson (1966) supposed that most Shetland Great Skuas pass into the North Sea in autumn and move south through the English Channel. Henderson (1974) suggests that after spending September in the North Sea, most Great Skuas then move into the Atlantic by passing round the north of Scotland between Orkney and Fair Isle. Seawatching from the Cherbourg peninsula indicates southward passage of Great Skuas out of the English Channel in autumn (Wooldridge 1974), which supports the ringing data as few recoveries have occurred in Ireland and West Britain after September. However, recoveries on the east North Sea coast occur mainly in October and November and none occur after December, yet in this month a number of birds are still in "home waters". This suggests that early dispersing birds enter the North Sea, and most move through the English Channel, while slowly dispersing birds tend not to leave home waters until November or December and then do so directly into the Atlantic, avoiding the North Sea in winter. Moore (1974) records a Great Skua passage in autumn through the Irish Sea, but the relative importance of this third route is unclear. Moore, Wooldridge and Henderson all recorded both Great Skua and Arctic Skua numbers on autumn passage. The proportion of Great Skuas was 11% in the Irish Sea, 13% in the English Channel and 10% in Aberdeenshire, suggesting that both species have similar patterns of movement past Britain in autumn.

The percentage of recoveries of first year birds in each geographical area in each month is shown in table 28. Monthly analysis of this sort assumes that recoveries occur within a short time of death. This is likely to be the case in a large pelagic species. An experiment which determined the time lag between death and recovery of auks was made by Hope-Jones, Howells, Rees & Wilson (1970), and indicated that most recoveries occurred within a month of death. As

Table 28. Percentages of recoveries of first year Great Skuas ringed in Shetland colonies and recovered in different geographical areas by the month of recovery. (All recoveries reported to the BTO before 31 December 1974 are included).

	Month						
	August	September	October	November	December	January	February to May
Number of recoveries	6	45	66	34	23	21	33
Area recovered (%)							
Home Waters	66	40	20	10	10	10	0
Wreck areas	0	10	10	5	5	0	0
East North Sea	0	20	40	40	15	0	10
East Atlantic	17	25	30	45	70	85	60
South of Europe	17	5	0	0	0	5	30

a large proportion of Great Skuas are recovered exhausted, caught or killed, the average time lag between death and recovery will be very short in this species, giving a clearer picture of seasonal geographical movements than is the case for many other species.

Few Great Skuas fledge before August, and all have flown by the end of that month. A few fledglings succeed in moving 3000 km from Shetland by the end of August, while others remain within a short distance of Shetland until December, so clearly dispersal in autumn occurs at a very variable rate. The fastest recorded movement is of an unfledged chick ringed on 8 July and caught on 30 August in the Canary Islands, so it must have covered about 150 km per day after fledging. September and October are the months of highest first year recovery rate, and presumably mortality, with wrecked birds being found in bad years in central Europe. The progressive southward movement is clear from the changes in table 28. This movement seems to continue until April, by which month most first year birds appear to have spread over the Atlantic from 50°N to the equator, with a few birds then returning to the North Sea, and a few south of the equator in April and May. There are few recoveries of one year old Great Skuas, suggesting a largely pelagic existence in the first summer. There appears to be a northward movement of at least part of the population, as there are recoveries in home waters and east North Sea areas in the period July to October (birds aged 1 year 0 months to 1 year 3 months). The bulk of the recoveries at this age, and all from November to February (up to the age of 1 year 7 months), occur south of latitude 50°N. Most are in the Iberian area, with a few further afield between Malta and Boston USA. The maximum dispersion appears to occur at this time in life, with the months March to May giving recoveries evenly divided between Home waters, east North Sea, Atlantic

and south of Europe, ranging from Shetland to Morocco, Mediterranean to the New World. During the summer (ages 1 year 11 months to 2 years 1 month), a few recoveries occur in the North Sea and East Atlantic, but most are found in Home waters or in Greenland, Iceland or Faroe. A return of many, but not all, birds to the East Atlantic occurs in November, and most winter recoveries are from this area, particularly in Iberia, until the age of three years, when a second spate of northerly recoveries occurs in the summer in Greenland, Norway and Faroe in particular, while a large number are also found in Shetland and Orkney. Winter recoveries again indicate movement to the area off Iberia, while a few recoveries south of Europe in both winter and summer indicate that even at this age (three years) some birds show no sign of returning to natal areas in the summer. Four year olds show virtually the same pattern as three year olds, with June recoveries in Faroe, Greenland and Spitsbergen as well as in Shetland and Orkney and also a few recoveries in West Africa, indicating the pronounced variation in behaviour within these age groups.

The tendency to visit latitudes north of the natal area wanes after this age, as does the tendency to visit the areas south of Europe. The establishment of a stable migration pattern is coincident with the attainment of maturity, as five, six and seven year old birds develop an attachment to a particular colony and establish themselves there to breed. Almost every recovery (48 of 49) of six year old or older birds in the months May to August, when breeding occurs, is in Shetland or Orkney. Autumn movements of adults result in winter recoveries, from September to April, occurring principally in the east Atlantic region, but also in Home waters and the east North Sea, areas which are virtually deserted by younger birds in these months. Thus winter movements of adults appear to be less extensive than those of

younger birds, as found in many other species.

This description of Great Skua migration is based almost entirely on ringing data. For this reason it is open to the bias inherent in the interpretation of recoveries. Thus a Great Skua migrating directly into the Atlantic, and spending the winter in the mid-Atlantic, as they are known to do (Jesperson 1930) would be most unlikely to be recovered at death. The 93% of Great Skuas which are not recovered could behave in this way, but transects of the North Atlantic by Wynne-Edwards (1935) also indicated that the Great Skua is primarily found on the east side of the Atlantic, so the lack of recoveries from the North American basin and the scarcity of recoveries from North and South America is only in part a reflection of low recovery chances, and partly due to the small number of Great Skuas which move that far west, of which most seem to originate from Iceland rather than Shetland, as nearly half the recoveries of Great Skua chicks ringed in Iceland are from the western side of the Atlantic (Collier & Stott 1976, Tuck 1971), suggesting that this population has a different migration pattern from the British population, and probably accounts for most of the Great Skua sightings in the west Atlantic (Brown, Nettleship, Germain, Tull and Davis 1975).

Return of prebreeders to the colony

Ringing data showed that a very few Great Skuas move towards, but do not reach their natal areas when only one year old, and only a small proportion return to natal areas in the summer of their second year, but virtually all return to breeding areas in the summer when five years old or older. Fortunately, the prebreeding Great Skuas do not mingle with breeding birds, but form discrete groups

called clubs (Perry 1948). The clubs of the Great Skua, unlike those of gulls (Tinbergen 1953) are on fixed and traditional sites, adjacent to or within each breeding colony. This feature allows the nonbreeding component of a colony to be studied as a distinct unit. Perry (1948) suggested that club birds include senile individuals, too old to lay, together with failed breeders and birds too young to breed. Potts (1961) attempted to break down the seasonal changes in numbers at the club in a Faroe colony into nonbreeders, potential breeders, off duty birds, failed breeders, postbreeders and prebreeders. These divisions were based only on numerical changes at the club through the season. On Foula, colour ringed birds are present, allowing estimation of the age structure of club gatherings. Chicks have been marked by Brathay Exploration Group expeditions with year-specific colour rings since 1968, but different numbers were colour ringed each year, and the proportion of the chicks colour ringed varies from year to year. An uncertain amount of ring loss has also occurred. The intensity of colour ringing also varied in different parts of the colony. For all these reasons, interpretation of observed proportions of colour ring combinations in a group of club birds is problematical. It has been estimated (section 1) that since 1968 between 3000 and 3500 chicks reached ringing age each year in the Foula colony. While the numbers monel ringed each year are exactly known, numbers colour ringed were not precisely recorded, but were roughly estimated. A second estimate of the proportion of ringed chicks which were also colour ringed may be obtained from recovery data. The difference between the two estimates (table 29) is partly due to loss of colour rings, but may be partly due to unreported presence of colour rings.

A second test for ring loss is given by comparing the proportions of recoveries of each cohort reported as also bearing colour rings,

Table 29. Estimates of the proportions of ringed chicks which were also colour ringed in each year, and the proportion of recoveries which were reported as also bearing colour rings.

Year	number chicks ringed	estimated number of chicks colour ringed	estimated percentage colour ringed	recoveries from this cohort	percentage of recoveries reported as colour ringed
1968	636	400	63	20	45
1969	1527	1000	65	66	39
1970	1155	800	69	25	32
1971	1577	900	57	40	18
1972	1726	700	41	22	23
1973	1354	800	59	14	29
1974	1666	700	42	19	32
1975	2224	900	40	14	21
1976	2110	1400	66	17	53

immediately after fledging, and several years later (table 30). This comparison, made by dividing recoveries into two approximately equal groups, suggests that, with most cohorts, there is loss of colour rings, but only the 1969 cohort shows a significant difference, possibly because the rings vary in dimensions from year to year, and some cohorts may be given better made colour rings than others, but partly also because 1969 gave more than twice as many recoveries as most other years. The 1970 and 1972 cohorts also show large differences in the percentages colour ringed between the two time periods, but sample sizes are too small in these years to give statistically significant results. Clearly some ring loss is occurring.

Assuming that, since 1968, 50% of ringed chicks were colour ringed, and 60% of all chicks on Foula were ringed, then 30% of all Great Skua chicks raised on Foula since 1968 should be colour ringed. If no ring loss and no immigration occurred, and no birds more than six years old visited clubs, then 30% of birds on clubs in 1974 should have been colour ringed. In fact, 26%, 23% and 24% were in three time periods in which counts were made in that year (table 31), suggesting that these conditions are not far from the truth.

Table 31. Percentage of birds with each colour ring combination on Flick club site through 1974.

Date of counts	number of birds counted	Percentage with each colour code; aged					
		total	6 yrs	5 yrs	4 yrs	3 yrs	2 yrs
July 1 - 14	100	26.0	6.0	6.0	8.0	6.0	0.0
July 15 - 31	200	23.0	3.5	4.5	7.5	7.0	0.5
Aug. 1 - 14	500	23.6	2.0	4.4	8.4	7.0	1.8

Table 30. Differences in the proportions of recoveries of each cohort of colour ringed chicks which were reported as colour ringed, showing the reduction due to ring loss.

Cohort	Years of recoveries	Number recovered	number colour ringed	percentage colour ringed	X_1^2, between time periods
1968	1968 - 1972	10	5	50	0.22, ns
	1973 - 1977	10	4	40	
1969	1969 - 1970	32	20	62	13.92, $p < 0.005$
	1971 - 1977	34	6	18	
1970	1970 - 1972	12	6	50	3.56, ns
	1973 - 1977	13	2	15	
1971	1971 - 1972	23	4	17	0.00, ns
	1973 - 1977	17	3	17	
1972	1972	11	4	36	2.40, ns
	1973 - 1977	11	1	9	

Counts through the 1973 season showed that the age structure of nonbreeding population on Foula changed through the season (table 32). Older birds arrived earlier than younger ones.

Table 32. Changes in the age structure of the club population at Flick during the 1973 breeding season.

Year ringed	age in 1973	percentage ringed with year colour combination on; 25.5	1.6	17.6	23.6	30.6	10.8
1968	5	11.2	9.0	4.7	2.0	1.5	2.0
1969	4	4.4	7.3	10.7	9.0	7.0	8.0
1970	3	1.2	1.7	3.0	7.0	8.5	8.0
1971	2	0.0	0.0	0.0	0.0	1.0	0.3
sample size		160	300	150	100	200	300

The youngest birds seen at breeding colonies are two year olds, which arrive at club sites at the end of June or during July. The same pattern was found in 1974 (tables 33 and 34), but in this year no two year olds were seen until mid-July.

Observations in 1976 indicated that a few birds colour ringed in 1968 (8 years old) were still regularly to be found on club sites, showing that some individuals do not establish territory until at least eight years old, as time budgets of breeders would not allow time for prolonged stays on club sites. The observation of 23 to 26% club birds with colour rings in 1974 suggests that all club birds are prebreeders, and also suggests that very little immigration occurs to Foula, as ring loss alone is sufficient to cause the reduction from a

Table 33. Ages of colour ringed individuals in samples observed at Flick club site in 1974.

Date of count	sample size	age of colour ringed individuals (years) 6	5	4	3	2
July 4	70	4	3	6	4	0
July 7	30	2	3	2	2	0
July 17	50	3	2	5	2	1
July 21	50	1	2	2	5	0
July 26	100	3	5	8	7	0
Aug. 1	100	3	5	7	6	1
Aug. 2	100	3	2	8	7	0
Aug. 3	100	1	7	8	4	2
Aug. 4	100	3	3	7	10	3
Aug. 10	100	0	5	12	8	3

Table 34. Ages of colour ringed individuals in samples observed at Kame club site in 1974.

Date of count	sample size	age of colour ringed individuals (years) 6	5	4	3	2
July 4	50	4	4	3	1	0
July 12	20	2	3	2	0	0
Aug. 2	35	0	2	3	1	1
Aug. 3	50	0	2	3	1	1
Aug. 10	40	0	2	3	3	2

predicted 30% of prebreeders with colour rings, and small numbers of seven and eight year old birds, too old to have been colour ringed, are also known to still be prebreeders.

Perry (1948) was incorrect to assume that clubs are largely composed of senile birds. There is no evidence from colour ring counts on Foula that breeders spend any time at clubs. Young (1963) considered that breeders visit clubs occasionally, but Burton (1968) never saw a breeding Brown Skua at Signy Island club sites, and Young (1972) later describes the club as a nonbreeding reserve, with no mention of its use by breeders.

Potts (1961) counted numbers on a Faroe club through 24 hour periods, showing an increase in numbers from an early morning minimum to a mid-afternoon peak, followed by a slight decrease, then an increase to a nocturnal plateau which was 25% greater than the mid-afternoon peak. Similar trends were seen at Foula clubs, but no counts were made over 24 hour periods. The main variation to this pattern was seen on foggy days, when numbers on the club remained very high throughout the 24 hours, suggesting that the nonbreeders do not attempt to feed in foggy weather. Potts (1961) claimed that all Great Skuas spend the night at the colony, so the number then present on clubs represents the total nonbreeding component of the population associated with the colony (ie. excluding the young nonbreeders which remain continuously at sea). It was not possible to count numbers at clubs at night through the season, so counts were made at mid-afternoon and it was assumed that these counts represented 75% of the nonbreeders present at night. In both 1975 and 1976, numbers at clubs increased steadily from early May to a peak around the beginning of July, then fell steadily to zero in early August. The peak of numbers at clubs coincides with the presence of two year old prebreeders in samples

examined for colour rings, indicating that numbers build up as younger birds return at progressively later dates to the colony. The decrease in numbers on clubs after early July is due in part to the departure of club birds to sea, but partly to the movement of the oldest club birds into territories, either at the edge of the club or at the edge of the colony.

In 1975 there were 23 club sites in the Foula colony, of which ten had not been used for more than two years, seven had been used for between three and ten years and six had been used for more than ten years. It was clear that the oldest clubs were occupied preferentially during May and June, and, in 1975, birds did not make use of the newest clubs until all the others were occupied by large numbers of prebreeders. This pattern (figure 8) implies that a saturation point is reached where the club becomes full, and further returning prebreeders are unable to gain entry. The limited size of most clubs, confined by surrounding breeding territories, and the aggressive nature of Great Skuas, even at clubs, gives a finite limit to the number of birds which can stand side by side. At most clubs this limit appears to be between 140 and 170 individuals.

Return of breeders to the colony

The first breeders to return to Shetland usually arrive at the breeding grounds at the end of March. In 1975 daily counts of Great Skuas on Foula were maintained from 28 March to 18 April to examine the buildup of attendance at the colony. The first individuals to visit the colony all did so around midday, and as numbers built up, the hours of attendance extended, with both earlier arrival and later departure, but no individuals remained on territory overnight until some date after 18 April (figure 9). The first birds to return did

Figure 8. Numbers of Great Skuas on club sites through the 1975 season on Foula. Peak afternoon counts for "incipient" clubs (a), new clubs (b), old clubs (c) and all clubs (d) are given for each weekly period, showing the seasonal increase in numbers to a peak in late July, and the tendency for old clubs to became saturated, after which numbers increase primarily in new clubs and finally incipient clubs form.

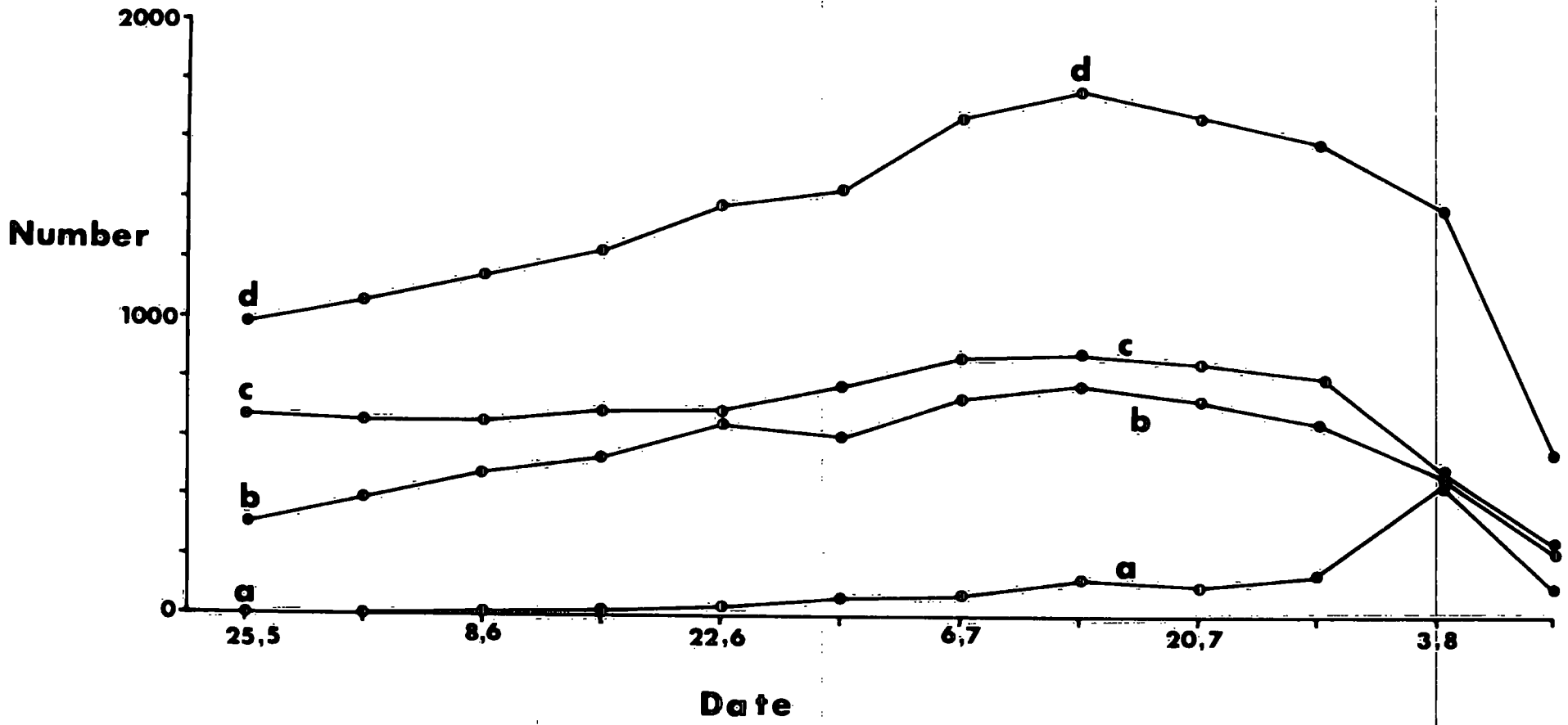
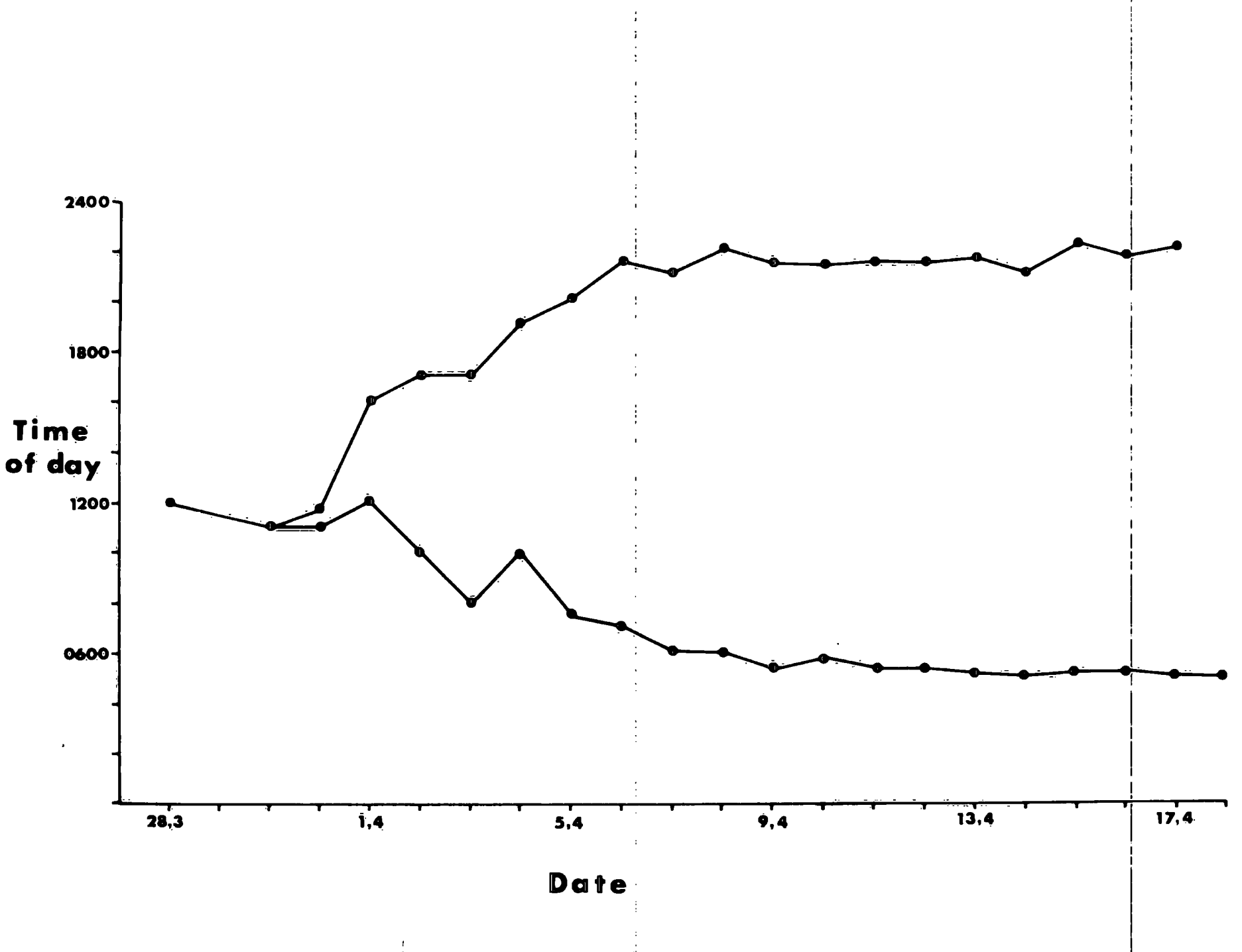

2000
1000
0
Number
d
d
c
c
b
b
a
a
25,5
8,6
22,6
6,7
20,7
3,8
Date

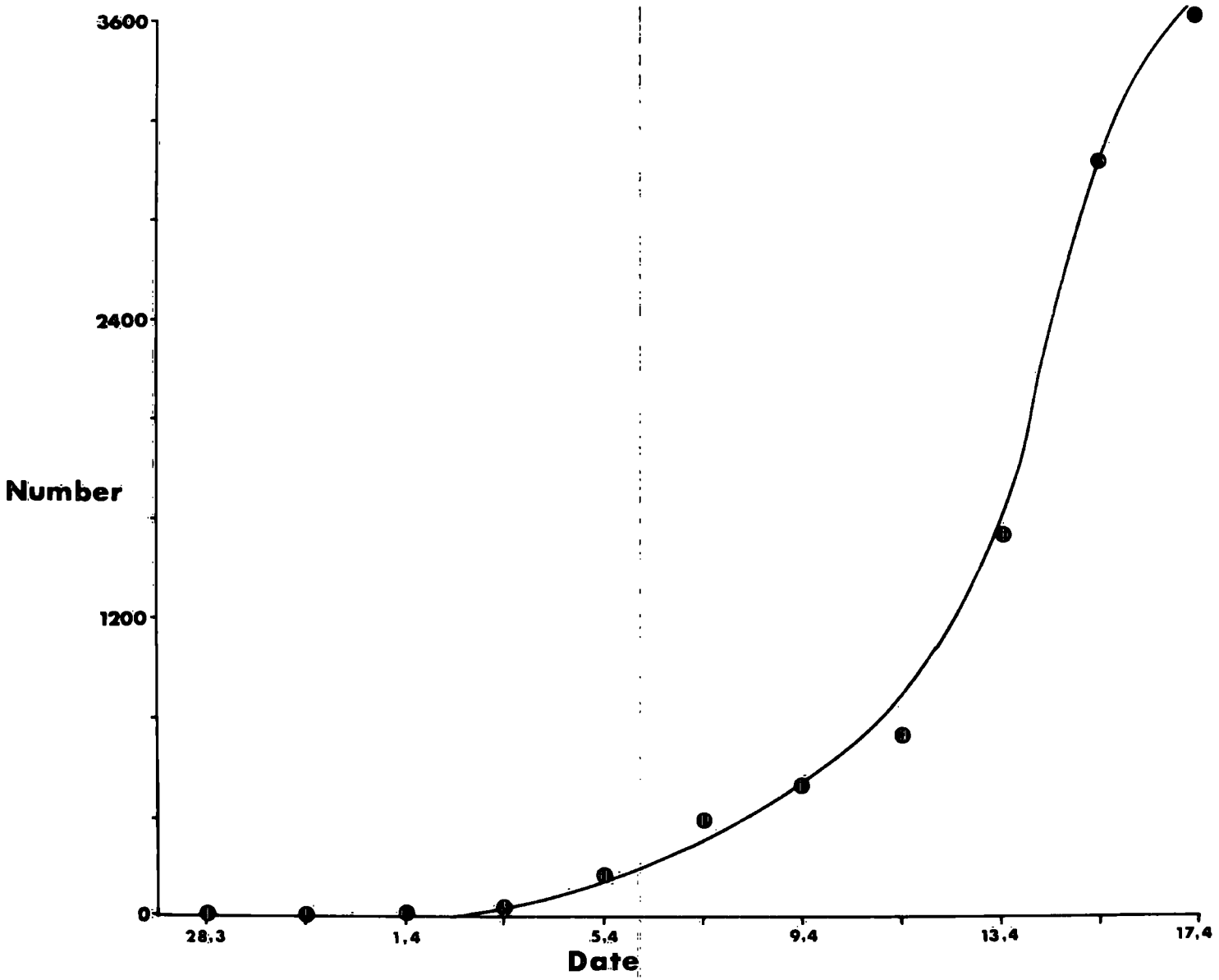
Figure 9. Times of day when Great Skuas were present on Foula during the first days of colony occupation at the start of the 1975 breeding season. Times of first and last sightings of individuals on the island each day are marked. Arrivals become progressively earlier and departures later after initial visits which all occur around mid-day.


2400
1800
1200
0600
Time of day
28,3
1,4
5,4
9,4
13,4
17,4
Date

not immediately re-establish their territories, but tended to soar around the island as a group, occasionally alighting on some area and taking part in communal displays which involved any number between two and 20 individuals. Often a bird settled beside another, forming a pair which then displayed to each other, but these pairs were transitory, and clearly, at this stage in the season, any bird was willing to display to any potential mate and in any part of the colony. Because of this mobility, it was impossible to determine whether older parts of the colony were re-occupied first, but this appeared not to be the case, as birds had been seen in every area of the colony after a few days. The number of individuals present increased rapidly towards mid-April, and 50% of the breeders were estimated to be back by 15 April (figure 10). Counts were terminated on 18 April, by which date no birds were yet present on any club site or bathing site, although most territories had been reoccupied.

The behaviour of Great Skuas returning to territories in a small part of the Foula colony, conveniently delineated by walls and cliff edge, was observed between 1 and 17 April. This area, in full view from the Brathay croft, called Ristie, was the best known part of the colony, and many breeding individuals have been known by colour rings or by individual characteristics for a number of seasons (most individuals in a small group can be distinguished by details of plumage as the colours of feathers are very variable between birds, often including odd white feathers in particular parts of the body). Sex of these birds was determined for most individuals by observation of copulations or of begging behaviour for food by females and the early season observations were interpreted in the light of these determinations. Birds were numbered by their order of arrival in the area, and territories numbered by the order of their occupation.

Figure 10. Maximum numbers of Great Skuas present on Foula each day at the start of the 1975 breeding season. By 15 April about 50 % of the breeding population (3000 birds of 3000 pairs) was present on Foula.


3600
2400
1200
0
Number
28,3
1,4
5,4
9,4
13,4
17,4
Date

On 9 April one bird landed at 1010, remaining on territory until 1400, and then departed. On 10 April the same individual, a male, arrived at 0811 and remained on territory until 1700. It was joined at 0920 by a female which remained with it until 1400. The spot that this pair occupied was the same territory in which they had bred together in previous seasons. A third individual, a male, arrived at 1100 and departed at 1400, having stood in a different part of the area for these three hours. At 2000 bird 1 returned, then left again at about 2100. At no time did I observe any behavioural interactions between these birds, but observations over these first few days were made only at 15 minute intervals through the daylight period. On subsequent days, periods of continuous observations were made, with periodic intervals of no observation. Behavioural postures of North Atlantic Great Skuas have been described in considerable detail by Perdeck (1960) and Burton (1970), and quantitatively analysed (Andersson 1974) in relation to motivational state by Andersson (1976). Studies of related species have also been made in detail, for the Brown Skua (Burton 1968, Hamilton 1934, Moynihan 1962, Stonehouse 1956), for the McCormick's Skua (Spellerberg 1971, Young 1963), for the Pomarine Skua (Andersson 1973), for the Arctic Skua (Perdeck 1963) and for the Long-tailed Skua (Andersson 1971). The terminology used in this study is taken from these works (table 35).

These ethological studies have been principally concerned with the motivation of skua displays and the relationships between these displays and those of other Larids. My interest in displays was in the functions of behaviour in determining the social organisation of Great Skua breeding colonies.

A total of 36 of the 41 Great Skuas which landed in the Ristie area during periods of observation totalling 60 hours between 11 April

Table 35. Names given to the principal ethological components of Great Skua display, together with their motivational significance where established.

Name used in this study	Symbol	Motivational significance	Name given by: Perdeck	Andersson	Moynihan	Burton
Long call	L	territorial	Long call	Long call	Long call	Long call
Wing raising	W	territorial	Wing raising	Wing raising	Wing raising	Wing raising
Oblique	O	territorial	Oblique	Oblique	High, normal or low oblique	High, normal or low oblique
Bend	B	aggressive	Bend	Bend	Very low oblique	Very low oblique
Bent Neck	Bn	aggressive	Bend	Bend	Bent neck	bent neck
Aggressive upright	Au	very aggressive	Aggressive upright	Neck forward	Aggressive upright	Upright
Intimidated upright	Iu	intimidated	Intimidated upright	Neck backward	Anxiety upright	Upright
Hunched	H	submissive	Hunched	Neck short Neck low	Hunched	Hunched
Circular parading	Cp	-	-	-	-	-

and 17 April 1975 had bred in the same area in 1974. A further three birds bred in this area for the first time in 1975, while the other two individuals only landed for a short time and were not seen again in this part of the island. The combination "Oblique/Wings raised/Long call" (OWL) was the most commonly adopted posture during these observations, but displays involving Aggressive upright (Au), Intimidated upright (Iu), Hunched (H) and Bent neck (Bn) postures were also common, as were Circular paradings (Cp), and a number of regurgitations were recorded, as well as a few overt attacks and other behavioural combinations based on the Bend and Oblique postures (table 36).

Table 36. Ethological units recorded during 60 hours of observation of Great Skuas on territories in the Ristie area of Foula between 11 April and 17 April 1975.

Ethological unit	Number of times recorded
Oblique/Wing raising/Long call	390
Aggressive Upright	131
Intimidated Upright	53
Circular parading	41
Hunched	39
Overt attacks	17
Bent neck	11
Bend/Wing raising	8
Regurgitation	6
Oblique/Wing raising	4
Bend/Wing raising/Long call	1
Bend	1

The Oblique/Wings raised/Long call complex is used by breeders on their territory to greet the returning mate, to communicate with neighbouring territory owners, with birds flying over the territory, and at the start of confrontations with intruders to the territory. This posture was adopted every time a bird entered a neighbour's territory, and was adopted by the territory owner(s) in 38 of 41 occasions in reply (table 37). It was used on almost every occasion that a bird returned to its territory to join its mate, and was usually adopted by birds returning to an empty territory, and in these cases it elicited a similar posture from a neighbouring bird on 24 of 44 occasions.

On 53 occasions the OWL display was used by a bird in response to fighting, displaying or courtship feeding in an adjacent territory, and it was often adopted in response to another Great Skua flying over the territory.

Several functions may be postulated for this display. It may cause social stimulation within the colony; Perdeck (1960) has already noted that its adoption by an individual on a club often generates group displaying in an infective way. Similar stimulation of neighbours was found in the Ristie territories, on 24 occasions when a bird displayed on return to its territory and stimulated a response from a neighbour, and on 53 further occasions resulting from general territorial activity (often mutual OWL displays by territory holder and returning mate). In this way it is probably similar to the 'choking' display of the Kittiwake (Cullen 1957) which spreads from bird to bird over short inter-nest distances.

Table 37. Occasions on which the Oblique/Wing raising/Long call (OWL) posture was adopted by territory owning Great Skuas observed at Ristie, Foula between 11 April and 17 April 1975.

Context	OWL adopted by:	number of occasions n	%
Return of mate	both of the pair	60	95.2
	male only	1	1.6
	female only	0	0.0
	neither bird	2	3.2
			100.0
Bird flying over territory	both of the pair	1	1.0
	male only	5	5.0
	female only	1	1.0
	neither bird	11	11.1
	male when present alone	55	55.6
	male did not respond	19	19.2
	female when present alone	4	4.0
	female did not respond	3	3.0
			99.9
Reaction to neighbour	display on return to empty territory	44	61.1
	no display on return to empty territory	28	38.9
			100.0
	response elicited from a neighbour	24	54.5
	no response elicited from a neighbour	20	45.5
			100.0
Intruder to territory	OWL by intruder	41	100.0
	no OWL display by intruder	0	0.0
			100.0

Table 37. Occasions on which the Oblique/Wing raising/Long call (OWL) posture was adopted by territory owning Great Skuas observed at Ristie, Foula between 11 April and 17 April 1975. - Continued.

Context	OWL adopted by:	number of occasions	
		n	%
Intruder to territory	Both residents reply with OWL	12	29.3
	Male only replies with OWL	1	2.4
	Female only replies with OWL	0	0.0
	Neither reply with OWL	3	7.3
	Male alone replies with OWL	23	56.1
	Female alone replies with OWL	2	4.9
			100.0
Courtship display between members of a pair	OWL posture adopted during display sequence	3	

SECTION 4

FOOD AND FEEDING

Limitations

Very little is known about the food and feeding of Great Skuas during their period of dispersal away from breeding colonies, which lasts from August to April. This study examines only the food and feeding of Great Skuas during the period of residence at breeding colonies, and the influences of these on the breeding of the species.

Theoretical analysis

In order to estimate the energy requirements of Great Skua populations during the period over which the birds are present at the breeding colony, a computer simulation model was developed. This uses generalised avian energetics parameters taken from the published literature, together with specific input parameters gathered by field observations on Foula, to calculate the energy requirement, in kilocalories, of breeders, nonbreeders and chicks for each day of the year that the birds are resident at the colony. Application of this model, with appropriate species-specific data sets, to each of the seabird species in turn, allows an analysis of energy flow through the Foula seabird community, showing the importance of the Great Skua population in utilisation of energy available to seabirds.

Several estimates of the food requirements of avian communities have been made. Belopolskii (1961) made empirical estimates by multiplying the mean weight of fish carried at each feeding trip by each seabird species, by the total number of feeding trips made per

day by each species population, to give the food requirements of each seabird population per day. Swartz (1966) used data on food consumption determined in captivity by Tuck & Squires (1955), or estimated in the field by Belopolskii (1961) and Uspenski (1956) to estimate the annual food consumption of adult seabirds at Cape Thomson colonies. Holmes & Sturges (1973) estimated the annual energy expenditure of the avian community of a northern hardwoods ecosystem by combining avian standing crop values with the metabolic energy expenditures predicted from the Lasiewski & Dawson (1967) standard metabolic rate equation for passerines, multiplied by a factor of 2.5 to allow for the energetic costs of activity. Holmes & Sturges, Swartz, and Belopolskii did not attempt to estimate the precision of their calculated community energy requirements, but were content to determine the order of magnitude of the energy flow through the avian component of the ecosystem. Holmes & Sturges (1973) concluded that only 0.1% of the primary production of the Hubbard Brook hardwood ecosystem was metabolised by the associated avian community. A similar but crude analysis of energy flow through the avifauna of the North Sea by Evans (1973), based on estimated summer and winter biomass totals of shorebirds, marine wildfowl and seabirds, combined with metabolic rates derived from the Lasiewski & Dawson (1967) nonpasserine equation, with allowances for foraging activity and reproduction, concluded that a minimum of 0.01% of the primary production was metabolised by the avifauna, representing a minimum of 10% of the energy input to the top carnivores (birds and predatory fish).

A detailed calculation of avian population energy requirements was made by Wiens & Innis (1974), using a computer simulation model. Their model uses census values of population density through the year, field or literature values for clutch size, mortality rates, repro-

ductive phenology and adult body weights, logistic growth equations for chicks, and an ambient temperature function. Existence energy requirements are computed using the Kend eigh (1970) equations, and energy costs of digestion, activity, moult, egg production and chick growth are added. The results are expressed per unit area. This model was used by Wiens & Scott (1975) to examine energy flow through the main species of the Oregon seabird community, and indicated that some 22% of the fish production of the area was utilised by the seabirds, Wiens & Innis (1974) examined the sensitivity of their model to parameter stress, but tested only their input parameters and not the basic energetics equations used in the simulation programme. They concluded that their model is robust, errors in most parameters giving a proportionately smaller error in the output values.

The model developed for this study is more sophisticated than previous ones in that direct calculations of the energy requirements of activity are made, using daily activity budgets for each species, and a confidence interval is calculated for the estimated total energy requirement of the population using a Monte-Carlo technique. A sensitivity analysis, altering one parameter at a time, is used to demonstrate which parameters most affect the output results, and comparison of the sensitivity of each input parameter with its standard error indicates where further fieldwork would most improve the precision of the model.

The simulation model used in this study can be divided into two sections. The first computes the size of the population present within the vicinity of the colony on each day of the year; numbers of breeding adults, prebreeding birds, eggs, chicks, and fledglings, and also calculates the values of other parameters which vary through the year (daily temperature and hours of feeding activity per day). It

is assumed (Fig. 11) that numbers of breeding adults increase linearly from the date of the first arrival of a breeder at the colony (D1) to the date on which the last breeding adult arrives (D2), and decrease linearly from the date on which the first breeder leaves the vicinity of the colony (D3) to the date on which the last breeder departs (D4). Nonbreeders are assumed to increase in numbers linearly from the date on which the first nonbreeder arrives (D5) up to a peak of nonbreeder attendance (D6), then decrease linearly to the date on which the last nonbreeder leaves the vicinity of the colony (D7). Fledglings are assumed to disperse from the colony at a uniform rate between specified dates (D8, D9), while hatching dates are assumed to be normally distributed with a mean date (XX). The range between the earliest and latest hatching dates recorded in the literature for Shetland is assumed to approximate to six times the standard deviation (XS) of the hatching dates, the total number of eggs hatching (XN) being equal to the area below the normal curve. Daily mean temperatures are taken from values given for Shetland by Irvine (1968). The mean number of hours spent per day in feeding activities (principally flight) is assumed to decrease linearly between specified dates (DA1, DA2) from a spring plateau level (ACT1) to a midsummer (usually pre-hatching) lower plateau (ACT2), then to increase linearly from date DA3 to date DA4 to a higher autumn/winter level (ACT3). Deviations from the assumption of linear arrival and departure are not likely to seriously affect the model output, as arrivals and departures occur over short periods compared with the total period that the population spends at the colony. For species which are present in the colony vicinity throughout the year, daily estimates of numbers of breeders and non-breeders are made by interpolating linearly between monthly mean counts.

Figure 11. Diagram of population submodal structure: seasonal changes in,

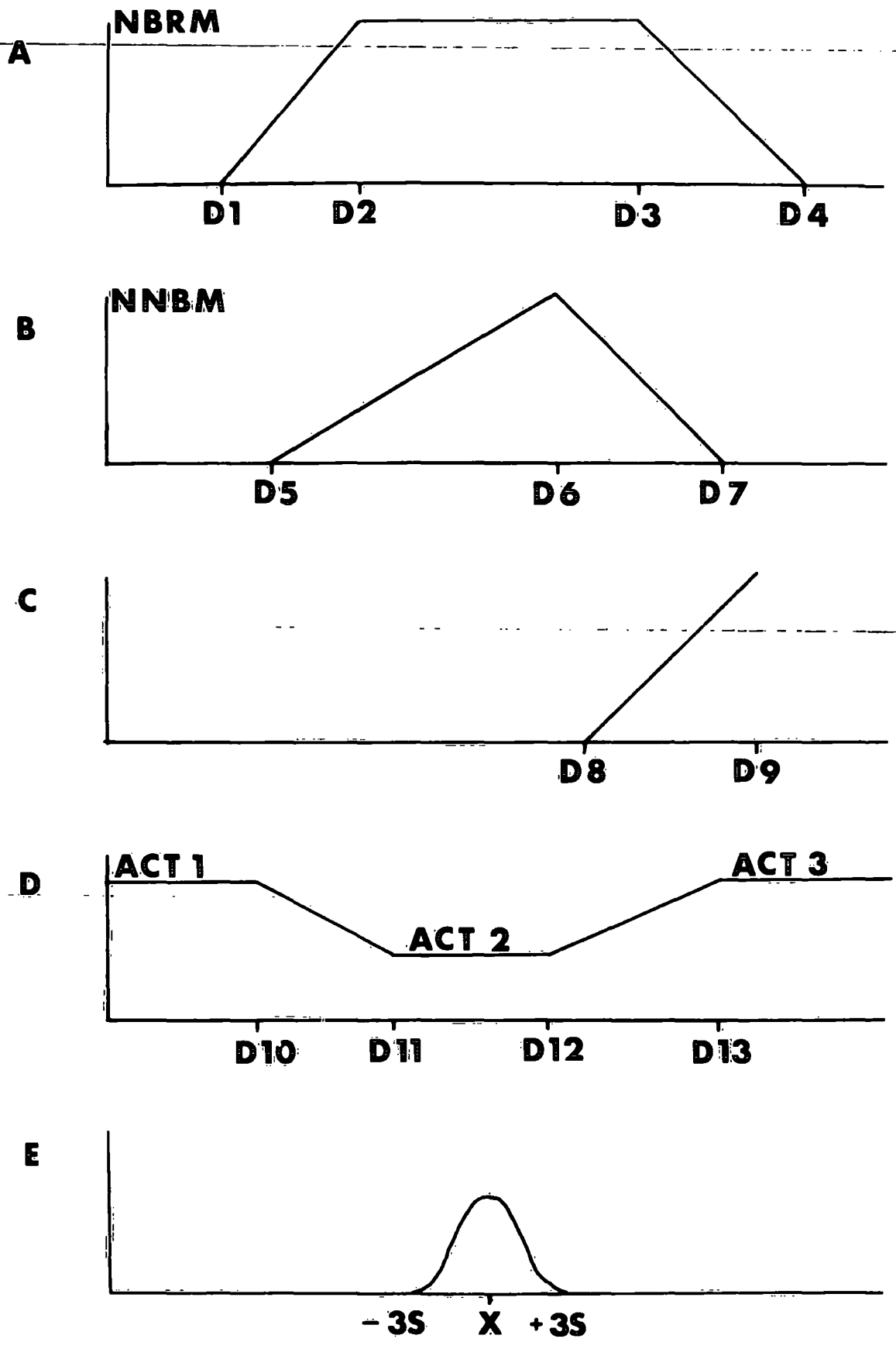
a) numbers of breeders

b) numbers of nonbreeders at the colony

c) proportion of fledglings which have dispersed from the colony

d) number of hours of foraging activity per day

e) number of chicks hatched per day

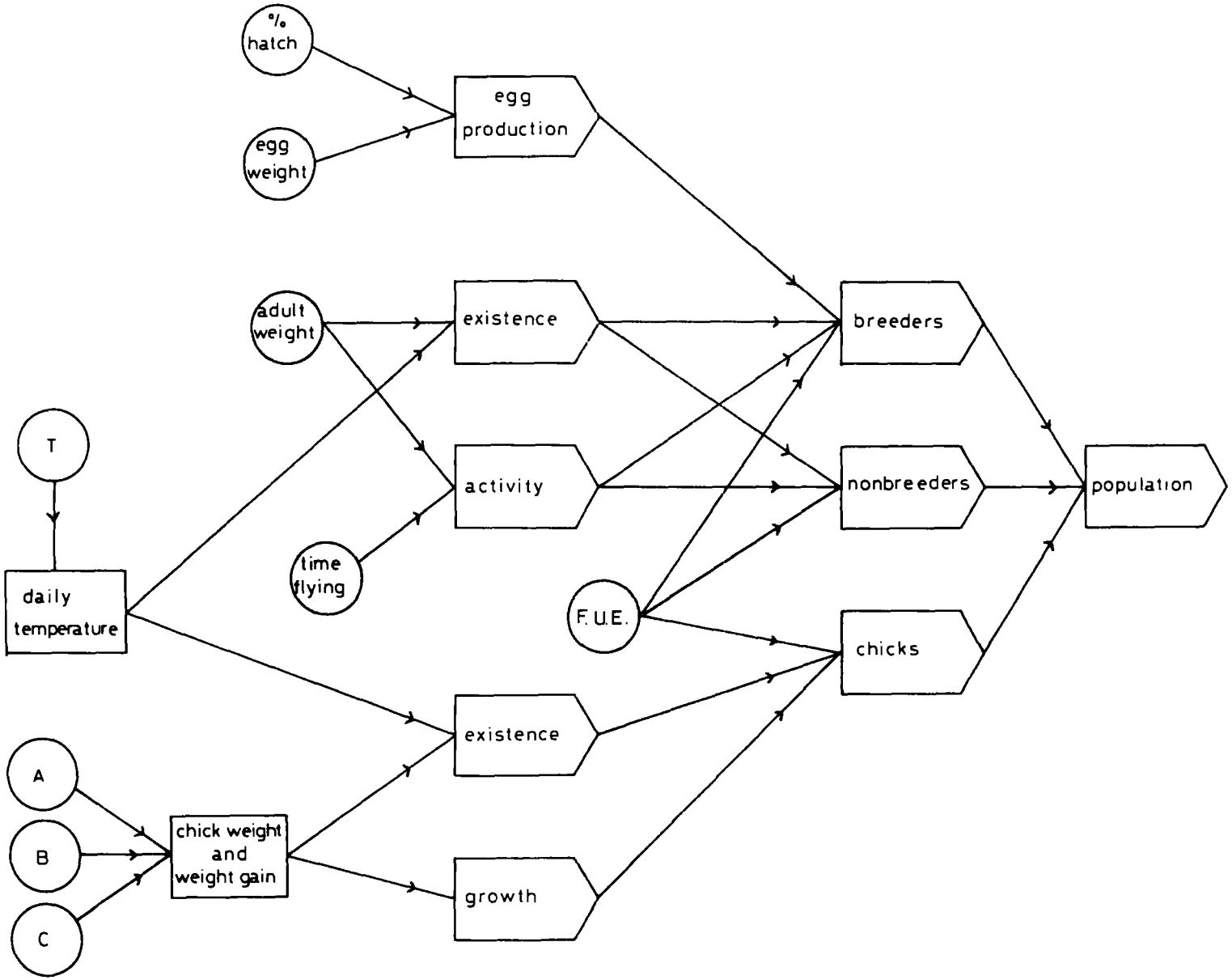

A
NBRM
D1
D2
D3
D4
B
NNBM
D5
D6
D7
C
D8
D9
D
ACT 1
ACT 2
ACT 3
D10
D11
D12
D13
E
-3S
X
+3S

Deviations from the assumptions in this section of the model can be summarised:

1. Hatching dates are usually approximately normally distributed, but are often skewed, reflecting the presence of large numbers of inexperienced breeders, and renesting attempts.
2. Considerable variations in the activity levels through the season are known to occur due to fluctuations in climatic parameters of food availability. Seasonal changes in activity budgets have received little attention and the exact form of the seasonal variation is uncertain, although apparently similar to the pattern used in the model for many species.
3. Survival rates of chicks between hatching and fledging are assumed to be 100%. In most seabirds chick mortality rates are low, but the model will slightly overestimate energy requirements of chicks. Chick and fledgling mortality are included in the estimate of dispersal rates of fledglings as these are calculated as the proportion of chicks remaining alive at the colony. The energy totals calculated also assume that no migration of seabirds from other breeding colonies occurs through the colony vicinity and that no other populations arrive in the colony vicinity to overwinter.

The second section of the model calculates the energy requirements of each category of the population (Fig. 12). The daily existence energy requirements of breeders, non-breeders, chicks and fledglings, are calculated from the Kend eigh (1970) equations, interpolating linearly between the values given by Kend eigh for existence energy requirements at $0^{\circ}C$ and $30^{\circ}C$. Thus the existence energy requirement at temperature T (EER_t) is calculated from equations

Figure 12. Diagram of energy submodel structure. Circles represent species input parameters; rectangular boxes, seasonally varying parameters; five-sided boxes, calculations of energy requirements of parts of the species population.


% hatch
egg weight
egg production
adult weight
existence
activity
breeders
nonbreeders
population
T
daily temperature
time flying
F.U.E.
chicks
existence
A
B
C
chick weight and weight gain
growth

$$EER_o = 4.337\ W^{0.53}$$

$$EER_{30} = 0.54\ W^{0.7545}$$

where EER_t is the energy in kcals day^{-1} expended in standard metabolism, specific dynamic action and limited locomotor activity, and W is the input value for body weight (in g). For breeders and nonbreeders body weight is the input value of the parameter AWT. For chicks and fledglings the value of W is calculated from the age of the chick using the logistic growth equation:

$$W = \frac{A}{1 + Be^{-C(t)}}$$

where t is the age of the chick in days from hatching, and A, B and C are growth constants for the species (Ricklefs 1968). The cost of egg production (EEP) is calculated from the freshweight of the egg at laying (EWT), the calorific value of the egg (CLEG), taken to be 1.3 kcals g^{-1} wet weight (Table 38) and the efficiency of egg production from body reserves (EPE), taken to be 73% (El-Wailly 1966; King 1973), using the equation:

$$EEP = (EWT)(CLEG)(100/EPE)$$

No allowance is made for the energy costs of moult, as few data are available on seabird moulting patterns, and it appears that this activity, which requires only a small increase over the daily energy costs, probably occurs primarily while the seabirds are dispersed or dispersing away from the colony. Costs of incubating the egg are also ignored as these are not readily calculated but are probably small

(Drent 1970). The daily energy requirement for chick growth ($ECGR_n$) is simply:

$$ECGR_n = (WTINC_n \times CLCH)$$

where WTINC is the weight increase of each chick since the previous day, and CLCH is the calorific value of chick tissues, taken to average 1.6 kcals g^{-1} wet weight.

Wind tunnel studies of flapping flight (Tucker 1973; Bernstein, Thomas & Schmidt-Nielsen 1973) and gliding flight (Baudinette & Schmidt-Nielsen 1974) have indicated that these increase the metabolic demand by six and two times the resting metabolic rate respectively. The resting metabolic rate may be taken as 1.7 times the standard metabolic rate (Baudinette & Schmidt-Nielsen 1974). The proportion of daily foraging activity spent in flapping rather than gliding flight (FL) has been used as a species-specific input parameter to calculate the energy requirements of activity (ERACT) from the following equations:

$$ERACT\ (flapping) = (ACT)(FL)(6 \times 1.7 \times SMR)$$
$$ERACT\ (gliding) = (ACT)(1 - FL)(2 \times 1.7 \times SMR)$$

$$ERACT\ (total) = ERACT(flapping) + ERACT(gliding)$$

where ACT is the average number of hours spent foraging away from the colony by adults each day. The value of ACT is allowed to vary seasonally (Fig. 11). All calculations are corrected to allow for the efficiency of food utilisation which is taken to be 80% (Pearson 1964; Dunn 1975).

Wiens & Innis (1974) used constant values in their model equations, which they derived from the literature. They subjected their model to a sensitivity analysis by altering the values of species-specific input parameters, but assumed errors in their equation constants to be relatively unimportant. My study was intended to examine where imprecisions in the stimulation model could be most readily and effectively reduced, so all values used were treated as variables. Thus two sets of input parameters can be described, the first set is of parameters which are model specific (Table 38). The second set is of parameters which are species-specific (Table 39). Standard errors have been calculated for each parameter in both sets. For the purposes of this study two sets of species parameter values have been used. These are for the Great Skua and for the Arctic Tern. The Arctic Tern was also included for detailed analysis as it contrasts with the Great Skua in its low body weight and high foraging activity, while it spends only three months at the breeding colonies. The two species therefore present rather contrasting data sets for model input.

The simulation model calculates the energy requirement in kilocalories, of the seabird population for each day of the year. Daily energy requirements for breeder existence, breeder foraging activity, chick existence and chick growth, and the total energy requirements of breeders, of nonbreeders, of chicks and of the entire population are output in a tabulated form and graphically (Figure 13).

As this model contains 44 input parameter values, many of which have large standard errors, it is important that the precision of output energy estimates should be determined. This precision depends both on the sensitivity of the model to parameter error, and the sizes of parameter standard errors. Sensitivity is here defined as the percentage change in the output value resulting from a one percent

Table 38. Model specific input parameters.

Model parameter	Mean	2SE as % of mean.	Sources
Shetland daily mean temperature	variable	0.2	1.
Food utilisation efficiency (%)	80.0	7.5	2,3,4.
Egg production efficiency (%)	73.0	13.7	5,6.
Calorific value of chicks (kcals/g)	1.6	18.8	7,8,9,10,11,12,13.
Calorific value of eggs (kcals/g)	1.3	15.4	6,14.
Resting/Standard metabolic rate	177	20.0	15,16,17.
Flapping energy requirement (xRMR)	6.0	16.7	15,16,18.
Gliding energy requirement (xRMR)	2.0	25.0	17.
Standard metabolic rate exponent	0.723	17.0	19.
Standard metabolic rate multiplicand	78.3	-23%, +30%	19.
Kend eigh equation A exponent	0.53	11.0	20.
Kend eigh equation A multiplicand	4.337	-32%, +40%	20.
Kendeigh equation B exponent	0.7545	5.6	20.
Kendeigh equation B multiplicand	0.54	-33%, +51%	20.

Sources: 1. Irvine (1968); 2. Pearson (1964); 3. Kale (1965); 4. Dunn (1975); 5. El-Wailly (1966); 6. King (1973); 7. Slobodkin & Richman (1961); 8. Odum, Marshall & Marples (1965); 9. Westerterp (1973); 10. Zimmerman (1965); 11. Ricklefs (1967); 12. Brisbin (1968); 13. Hulscher (1974); 14. Schreiber & Lawrence (1976); 15. Tucker (1973); 16. Bernstein, Thomas & Schmidt-Nielsen (1973); 17. Baudinette & Schmidt-Nielsen (1974); 18. LeFebvre (1956); 19. Lasiewski & Dawson (1967); 20. Kendeigh (1970).

Table 39. Species specific input parameters used to test the model.

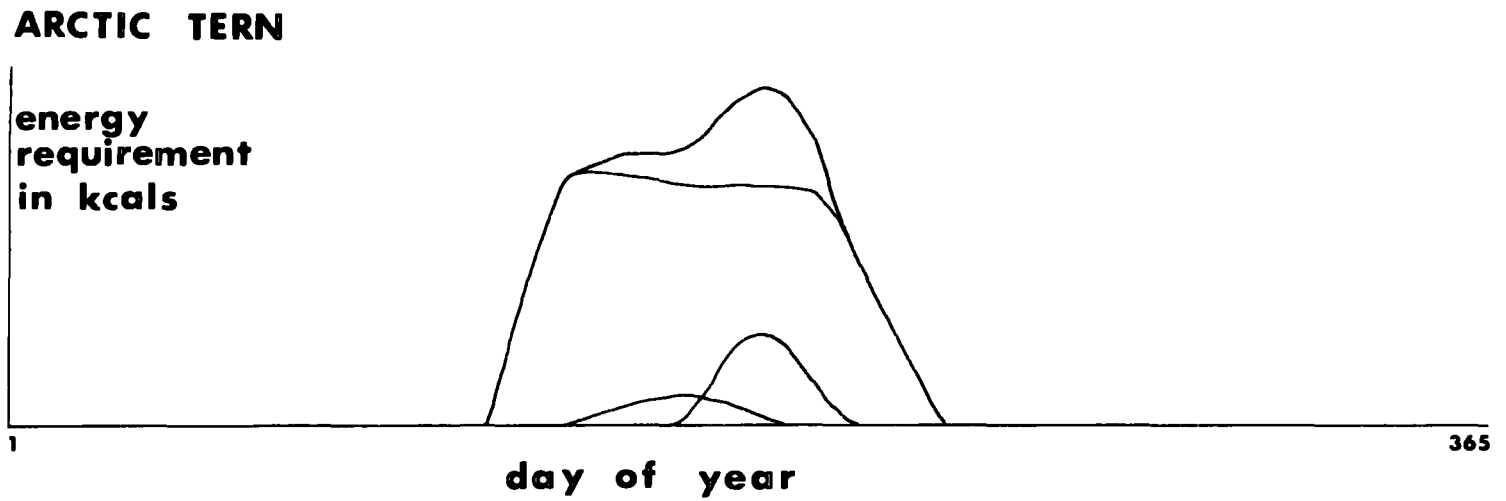
Input parameter name	Parameter label	Species Data: Great Skua mean	Great Skua 2SE as % of mean	Arctic Tern mean	Arctic Tern 2SE as % of mean.
Adult body weight (g)	AWT	1400.0	7.1	105.0	10.0
Hatching success (%)	HS	75.0	6.7	75.0	10.0
% flapping flight	FL	50.0	40.0	100.0	0.0
Logistic growth asymptote	AA	1167.08	1.5	111.48	5.0
Logistic growth constant	BB	16.955	0.9	7.575	5.0
Logistic growth rate	CC	0.176	2.8	0.288	5.0
Incubation period (days)	IP	29.0	1.7	22.0	3.0
Egg weight (g) at laying	EWT	96.0	1.0	18.0	5.0
Number of days of chick growth	NDFL	40.0	1.2	25.0	5.0
Date of first breeder arrival	ID1	85	3 days	121	2 days
Date of last breeder arrival	ID2	115	5	140	4
Date of first breeder departure	ID3	213	5	201	4
Date of last breeder departure	ID4	283	6	232	3
Date of first nonbreeder arrival	ID5	127	6	140	5
Date of nonbreeder peak numbers	ID6	189	3	170	5

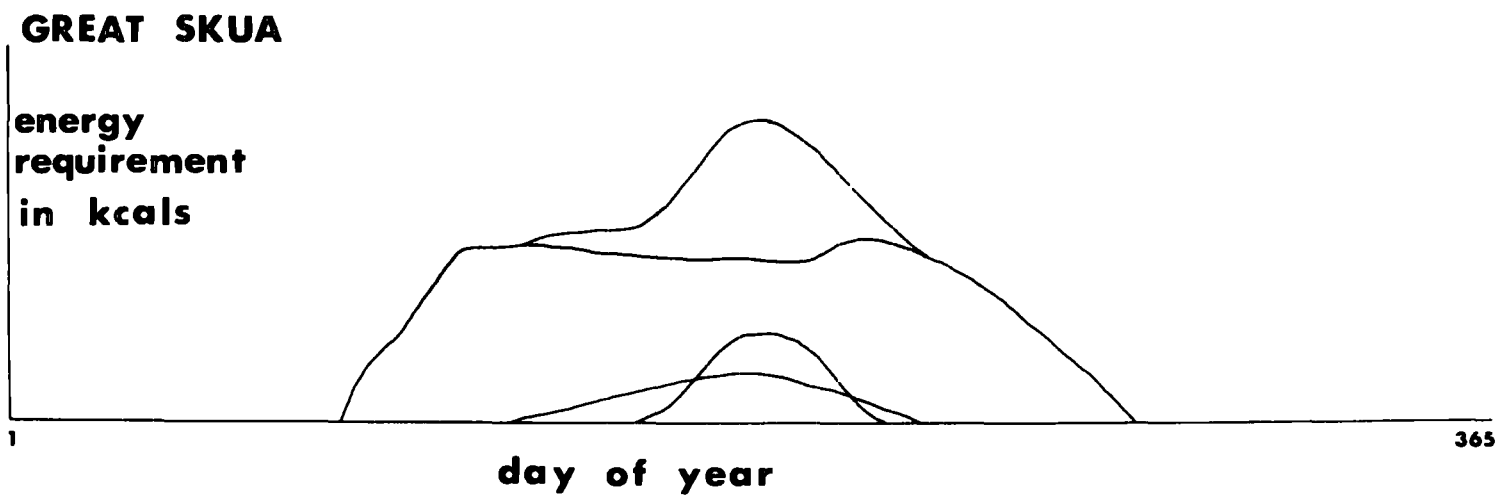
Table 39. Species specific input parameters used to test the model, - continued.

Input parameter name	Parameter label	Species Data: Great Skua mean	Great Skua 2SE as % of mean	Artic Tern mean	Artic Tern 2SE as% of mean
Date of last nonbreeder departure	ID7	230	3	200	5
Date of first fledgling dispersal	ID8	213	4	200	4
Date of last fledgling dispersal	ID9	253	4	230	3
Peak number of breeding birds	NBRM	6000	5.0	11300	15.0
Peak number of nonbreeding birds	NNBM	2000	10.0	1500	50.0
Mean hatching date	XX	168.0	0.6	176.0	2.0
Standard deviation of XX (days)	XS	6.0	3.3	5.0	20.0
Number of chicks hatched	XN	3990	7.3	8899	20.0
Activity level date one	IDA1	85	3 days	121	2 days
Activity level date two	IDA2	100	5	140	4
Activity level date three	IDA3	200	5	200	5
Activity level date four	IDA4	283	6	230	4
Hours active feeding per day during activity period one	ACT1	10.0	20.0	10.0	50.0
during activity period two	ACT2	2.0	25.0	8.0	50.0
during activity period three	ACT3	12.0	16.7	12.0	50.0

Sources: Furness (unpubl.), Jackson (1966), Cramp et al. (1974), Baxter & Rintoul (1953), Venables & Venables (1955), Fisher & Lockley (1953), Annual Stottish Bird Reports, Annual Fair Isle Bird Observatory Reports, Annual Shetland Bird Reports.

Figure 13. Model output of daily energy requirements for a) Arctic Tern and b) Great Skua on Foula. The curves represent, in order of increasing energy requirement, nonbreeders, chicks, breeders, and the entire population.


ARCTIC TERN
energy
requirement
in kcals
1
365
day of year


GREAT SKUA
energy
requirement
in kcals
1
365
day of year

change in the value of an input parameter. The values of the sensitivity of each parameter for a particular species are obtained by running the model 44 times, with one input paremeter at a time increased by 1%. For the sensitivity of the estimate of the energy requirement of the entire population per annum, parameter sensitivity values vary from 0.00 up to 2.40 for the two species tested. Clearly errors in some parameter values (those with high sensitivity values) have much greater effects on the precision of the output results than errors in other parameter values. It is also clear that the sensitivity values obtained differ between species for the same parameters (Tables 40 and 41). Thus the model is more sensitive to errors in the activity levels of Arctic Terns (ACT2 sensitivity of 0.416) than of Great Skuas (ACT2 sensitivity of 0.092). This is to be expected, as Arctic Terns spend considerably more time foraging, so this represents a large proportion of the energy expenditure of the population, while the small amount of time spent in foraging by Great Skuas means that this forms only a small part of the population energy expenditure of this species. Determination of sensitivity values shows which parameters must be precisely known if output results with small standard errors are to be obtained. The majority of sensitivity values are small (Figures 14 and 15), so that sizes of the standard errors of the few parameters with large sensitivity values will primarily determine the precision of the output results.

Multiplying the sensitivity values by twice the standard errors of input parameters gives the expected maximum output error resulting from each single input parameter error (Tables 40 and 41). These output errors measure the error in output total if one parameter is set at the 95% confidence limit for that parameter while all other parameters remain at their mean values. For the Great Skua (Table 40),

Figure 14. Model sensitivity to errors in the 44 parameters for Great Skua input data. Sensitivity of 1.0 means that a 1% error in that input parameter results in a 1% error in the output estimate.

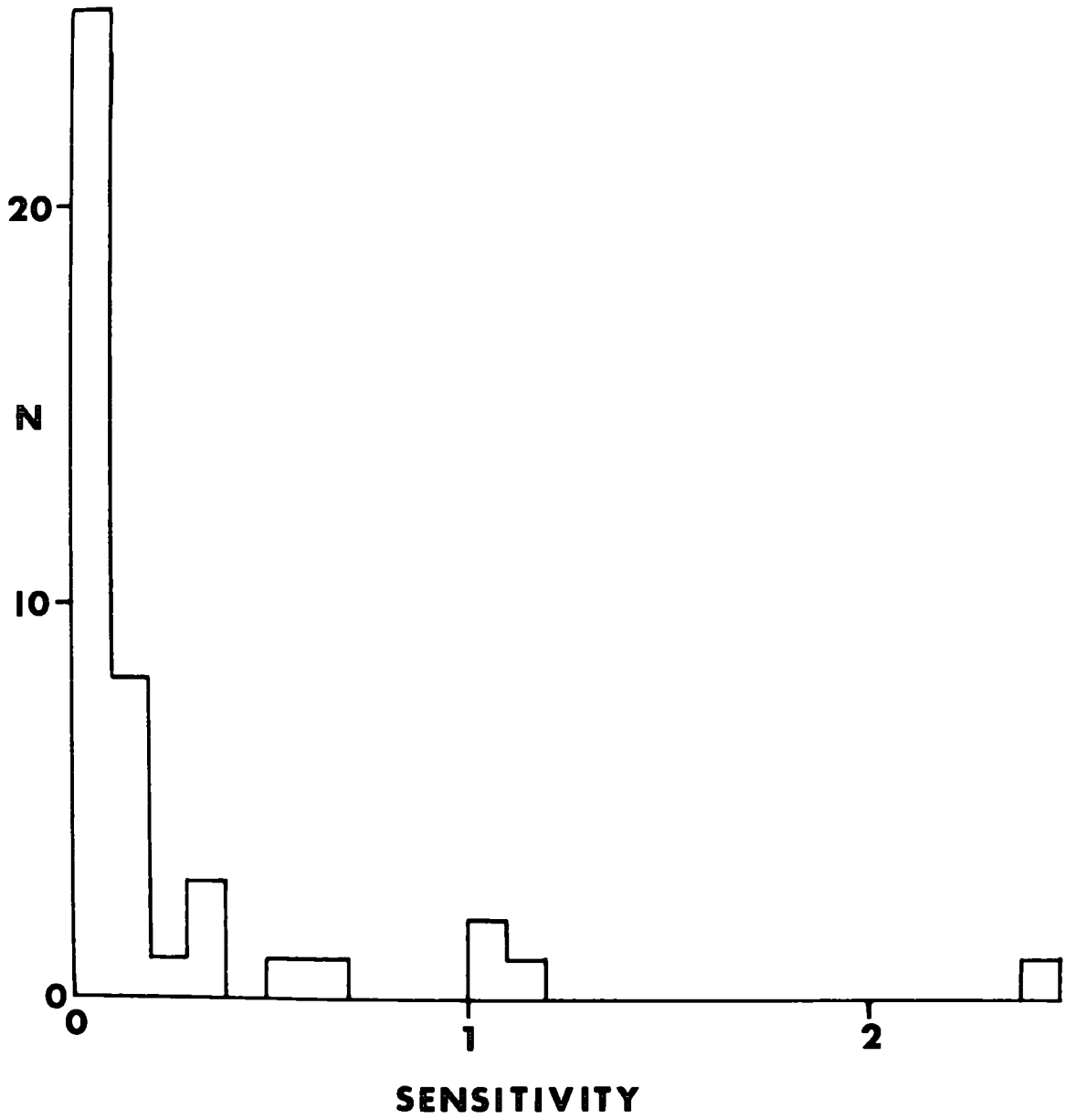
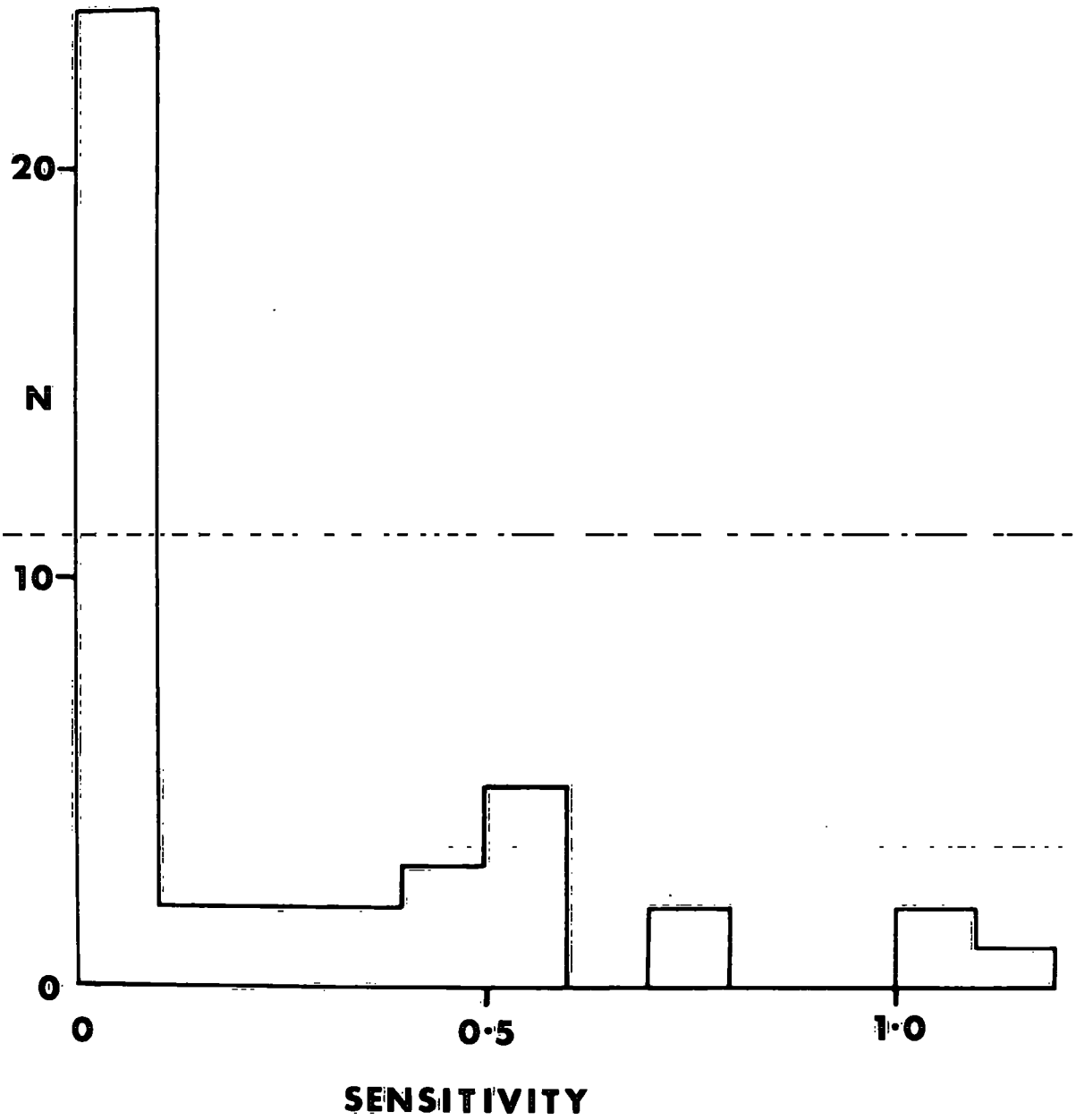

20
N
10
0
0
1
2
SENSITIVITY

Figure 15. Model sensitivity to errors in the 44 parameters for Arctic Tern input data.


20
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1·0
SENSITIVITY

Table 40. Analysis of model using Great Skua input parameter set.

Parameter	2SE as % of mean	model sensitivity to the parameter	output error resulting
Kendeigh equation A exponent	11.0	2.400	26.40
Kendeigh equation A multiplicand	38.0	0.620	23.56
Kendeigh equation B multiplicand	42.0	0.180	7.56
Food utilisation efficiency	7.5	1.000	7.40
Kendeigh equation B exponent	5.6	1.100	6.16
Numbers of breeders, nonbreeders and chicks	6.0	1.000	6.00
% of foraging spent in flapping flight	44.0	0.110	4.40
SMR multiplicand	27.0	0.160	4.32
Adult body weight	7.1	0.540	3.83
Energy requirement of flapping flight	16.7	0.160	2.67
Hours activity per day during period two	25.0	0.092	2.30
Date of last breeder departure (ID4)	6 days	0.380	2.28

All other input parameter errors result in output errors of less than 2.0 %.

Table 41. Analysis of model using Arctic Tern input parameter set.

Parameter	2SE as % of mean.	model sensitivity to the parameter.	output error resulting.
Hours activity per day during period two	50.0	0.416	20.30
Numbers of breeders, nonbreeders and chicks	20.0	1.000	20.00
Kendeigh equation A multiplicand	38.0	0.423	16.07
SMR multiplicand	27.0	0.481	12.99
Kendeigh equation A exponent	11.0	1.171	12.18
SMR exponent	17.0	0.723	12.29
Energy requirement of flapping flight	16.7	0.579	9.67
Food utilisation efficiency	7.5	1.000	7.50
Adult body weight	10.0	0.580	5.80
Energy requirement of gliding flight	25.0	0.193	4.82
Kendeigh equation B multiplicand	42.0	0.076	3.19
Hours activity per day during period three	50.0	0.044	2.20
Date of first breeder departure (ID3)	4 days	0.547	2.19
Date of last breeder departure (ID4)	3 days	0.721	2.16
Date of last breeder arrival (ID2)	4 days	0.522	2.09

All other input parameter errors result in output errors of less than 2.0 %

the Kendeigh equation A exponent has both a very high sensitivity and a high standard error, resulting in an output error value of 26.40 in other words the estimated annual energy requirement of the Great Skua population may err by up to ± 26.4 % of the value output by the model as a result of the error in the input value of the Kendeigh equation A exponent alone. Other parameters, either because they have smaller sensitivity values, or smaller standard errors, or both, have much smaller effects on the output error for this species. For the Arctic Tern (Table 41) the sensitivity value of the Kendeigh equation A exponent is considerably smaller, so the resultant output error value is reduced to 12.88. Differences in sensitivity values and standard errors result in a different set of parameters which critically affect the output precision of runs for different species. Analysis of this type for each seabird species will allow the parameters causing most of the error in output results to be identified, so that further research may be directed at reducing the standard errors of these parameters to give more precise output values.

It has not been possible to derive actual values for the standard errors of the output results from the results of the sensitivity analyses, as it is most unlikely that all parameter errors will be in the same direction. Some errors will tend to cancel out, while others combine, possibly additively, possibly synergistically. In order to obtain exact values for the standard errors of output estimates the model was analysed using a Monte Carlo simulation technique. A computer function was employed to generate random numbers. These were then used to seed a second function, which, using input values of mean and standard deviation, generates normally distributed random variables. These routines were called to return values for each of the 44 input parameters, and these altered values were then input to

the model, which calculated the energy requirements as before. The difference between the output estimate from this run and the estimate from a run with all parameters assuming their mean values as a measure of the variance of the output estimate. The Monte Carlo analysis comprised 300 runs of the model for each species, each run using a unique set of modified values, altered from the means by the random number generations. The results of this analysis (Table 42) show that the estimate of the annual energy requirement of the entire Great Skua population is 31.345×10^7 kcals with a standard deviation of 8.800×10^7 kcals. The 95% confidence interval for this estimate ranges from 14.1×10^7 to 48.6×10^7 kcals. While the two species chosen for this analysis were of markedly different types, it is worth noting that the coefficients of variation of the population energy requirements are virtually the same, suggesting that the model may give similar precision for the available parameter sets of most seabird species.

The Monte Carlo analysis showed that the 95% confidence interval for the energy requirements of both species populations examined ranged over $\pm$ 50% of the mean estimate. The sensitivity and output error analyses showed that this confidence interval was largely due to errors in a small number of the input parameter values. In particular, the Kendeigh (1970) equations resulted in large output error values (Tables 40 and 41). Pimm (1976) reanalysed the data used by Kendeigh (1970) and found that the use of dummy variables in a stepwise multiple regression analysis of existence energy requirements of passerines in relation to ambient temperature, body weight, and photoperiod explained considerably more of the variance than the equations furnished by Kendeigh (1970). The use of Pimm's equation for passerines, and the calculation of a similar equation for nonpasserines,

Table 42. Results of a Monte Carlo simulation analysis of the precision of output estimates of energy requirements (per annum). (Means and standard deviations x 10^4).

Parameter for which energy requirement was estimated:	Energy requirement estimates for each species: Great Skua mean	Great Skua standard deviation	Great Skua coefficient of variation	Arctic Tern mean	Arctic Tern standard deviation	Arctic Tern coefficient of variation
Breeders; existence	18806	5735	30.5	4563	1271	27.9
Breeders; activity	6770	2465	36.4	5178	2027	39.1
Breeders; egg1production	115	11	9.6	47	6	12.8
Breeders; total	25692	7394	28.8	9790	2839	29.0
Nonbreeders; esistence	2144	654	30.5	202	8080	39.6
Nonbreeders; activity	558	210	37.6	224	119	53.1
Nonbreeders; total	2700	792	29.3	426	182	42.7
Chick; existence	2111	613	29.0	837	242	28.9
Chick; growth	843	86	10.2	168	27	16.1
Entire population	31345	8800	28.1	11224	3180	28.3

would considerably increase the precision of this, and similar energetics models, all of which presently rely on Kendeigh's equations. Further gains in precision would be obtained by reducing standard errors in the estimated values of food utilisation efficiency, adult body weights, the proportion of foraging time spent in flapping flight, and the mean number of hours of foraging per day. All these parameters could readily be examined in a range of species, in the field or laboratory as relevant. Having obtained further estimates of these values, the energy costs of moult and incubation could be incorporated into the model as a further refinement. Eventual reduction of output confidence interval limits to ± 20% should be possible, below which further progress would be impeded by the lack of sufficiently precise estimates of the numbers of each seabird species in a colony.

This study indicated that the energetic cost of activity was a 36% addition to the total existence energy costs for Great Skuas, and a 113% addition to the existence costs of Arctic Terns. These are probably near the extreme values for seabird species, but indicate the inaccuracies inherent in the addition of a constant proportion of the existence energy cost to allow for activity costs. A comparison of the estimated additional costs of activity used in previous published models of energy requirements of avian communities is given in Table 43. These values range from 0% to 100% of the existence cost, but generally appear to underestimate activity costs estimated from directly determined parameter values, although for passerines activity costs may be relatively lower as thermoregulation costs will be relatively greater than those of seabirds.

This model has been used to estimate the annual energy requirement of each seabird species in each of the main Shetland seabird colonies. Differences in the seasonal energy requirement envelope

Table 43. Estimates of the increase in energy requirement above the existence level resulting from daily activity.

Source	% increase over existence metabolism	avain group or species
Weiner & Glowacinski (1975)	0	passerines
West & DeWolfe (1974)	13	passerines
Holmes & Sturges (1973)	19	passerines
Wiens & Innis (1974)	40	passerines
Wiens & Scott (1975)	40	seabirds
Evans (1973)	100	seabirds
this study	36	Great Skua
this study	113	Arctic Tern

of each species may indicate competitive displacement of breeding phenologies. Similar displacements occur within species (e.g. Fig. 13) in the peak energy requirements of breeding, nonbreeding and chick categories of the population. Summation of the population energy requirements of each species gives the annual energy flow to seabirds in the colony vicinity. Coupling of this calculation with estimates of energy flow through the marine food web allows the importance of seabirds in marine ecosystems to be assessed. The analysis of energy flow to seabirds at Foula, is given below. It is assumed that all foraging occurs within 45 km of the colony, a distance considerably greater than was travelled by auks, Shags, Kittiwakes or terns studied by Pearson (1968), or the distances from breeding colonies at which auks were seen by Cody (1973) or Bedard (1976), who suggest that most foraging during the breeding season occurs within 20 km of the colonies. The circles of 45 km radius (Figure 16) intersect with circles around adjacent colonies, and also contain areas of the main Shetland islands, on which small numbers of seabirds breed. Portioning half of the area of circle overlap to each colony, and subtracting the area of land within the circle, leaves 4700 km^2 of sea over which Foula seabirds can forage, out of a total area of 6362 km^2 within the 45 km radius. Numbers of breeding individuals, and the maximum number of nonbreeding individuals occurring within the colony vicinity during the breeding season, are given for each species in Table 44. Energy requirements of each seabird species in the Foula community over the period which they spend in the colony vicinity, are given in Table 44. A small amount of the total energy requirement of 1.235×10^{10} kcals yr^{-1} is provided by zooplankton. Perhaps the bulk of the Storm Petrels' energy

Figure 16. The four main seabird colonies in Shetland, showing circles of 45 km radius round each colony, within which all foraging is assumed to occur. It is assumed that seabirds do not cross land during foraging trips away from the colony.

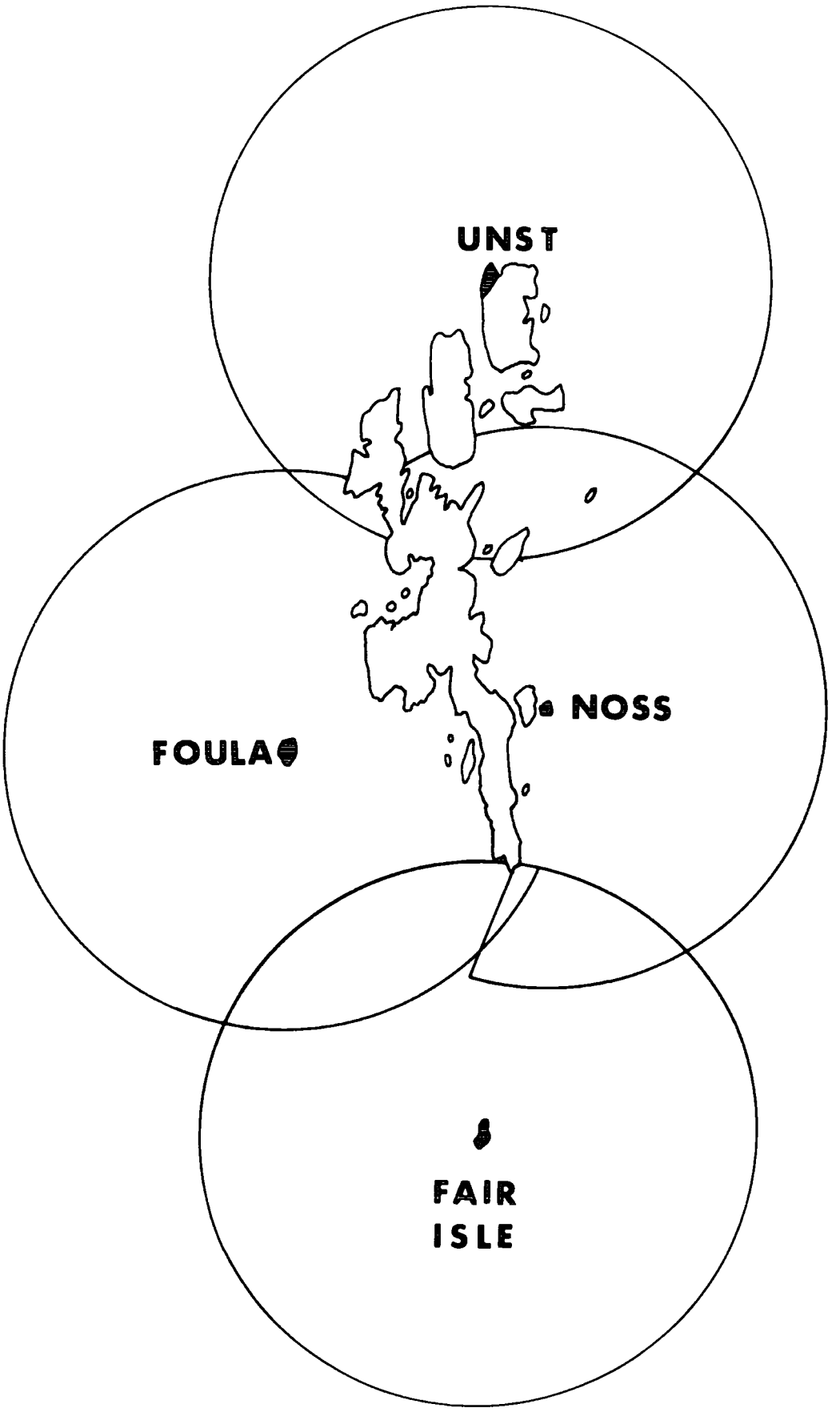
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Table 44. Energy requirements of seabird populations of Foula, Shetland over the period during which the birds are present in the vicinity of the colony; species are ranked according to total energy requirement.

Species	Nomenclature	Number of breeding individuals	Maximum number of nonbreeding individuals in colony area	Population energy requirement ($kcals \times 10^6$ per year)
Fulmar	*Fulmaris glacialis* (L.)	40 000	18 000	4 802.9
Guillemot	*Uria aalge* Pontopp.	40 000	15 000	2 675.0
Shag	*Phalacrocorax aristotelis* (L.)	6 700	2 000	1 943.0
Puffin	*Fratercula arctica* (L.)	60 000	20 000	1 614.7
Kittiwake	*Rissa tridactyla* (L.)	11 140	1 000	426.1
Great Skua	*Catharacta skua* Brunnich	6 000	2 000	331.4
Razorbill	*Alca torda* (L.)	6 000	2 000	268.6
Arctic Tern	*Sterna paradisaea* Pontopp.	11 300	1 500	119.5
Storm Petrel	*Hydrobates pelagicus* (L.)	6 000	3 000	54.2
Great Black-backed Gull	*Larus marinus* (L.)	44	500	47.1
Herring Gull	*Larus argentatus* Pontopp.	46	500	25.0
Gannet	*Sula bassana* (L.)	0	500	17.7
Black Guillemot	*Cepphus grylle* (L.)	240	80	15.3
Arctic Skua	*Stercorarius parasiticus* (L.)	600	200	11.1

requirements and part of the Fulmars' requirements may be provided by zooplankton, so the total energy requirement from fish may be only 1.2×10^{10} kcals yr^{-1}. The 95% confidence interval of the total requirement for each species, of ± 50% of the mean, is due largely to imprecisions in model parameters, so errors will be in the same direction in each species calculation. The 95% confidence interval for the energy requirement of the entire seabird community is therefore not likely to be much less than ± 50%; i.e. ranging between 0.6×10^{10} and 1.8×10^{10} kcals yr^{-1}. The production of fish in Shetland waters has not been studied in detail, but a number of estimates of primary production and fish production in various areas, including the North Sea are available (Table 45). While Ryther (1969) considered that the short, and therefore efficient, food chains found in areas of upwelling, give annual fish production many thousands of times greater than found in oceanic ecosystems, there appears to be little difference in the structure of food webs in different parts of the North Sea (Raymont 1963) so such differences would not be expected over this particular area. Cushing (1975) emphasised the greater transfer coefficients (food utilisation efficiencies) found in conditions of low primary production, so that, with the same food web, a tenfold range of primary production results in only a threefold difference in fish production. The extreme estimates of primary production in North Sea areas range between 540 and 1350 kcals m^{-2} yr^{-1}. It seems probable that the primary production around Shetland is greater than the average for the North Sea area, as some upwelling and considerable mixing of currents occurs off Shetland, but primary production probably falls within the limits of 600 to 1300 kcals m^{-2} yr^{-1}, resulting in fish production of 6 to 12 kcals m^{-2} yr^{-1}. Taking these values as limits, the total fish production in the 4700 km^2 area utilised by

Table 45. Estimates of primary production and fish production (kcals m^{-2} yr^{-1}) in different marine areas.

Area	Primary production	Fish production	Efficiency of fish production from primary production	Author
Upwelling	3 000	270.0	9.0%	Ryther (1969)
Coastal	1 000	3.4	0.34%	
Oceanic	500	0.005	0.001%	(global analysis)
Peru current	36 000	-	-	Menzel et al. (1971)
Long Island Sound	4 700	-	-	Riley (1956)
Georges Bank	1 200 - 3 000	-	-	Steele (1956)
Sargasso Sea	1 340	-	-	Menzel & Ryther (1961)
North Sea	800	8.0	1.0%	Steele (1974)
North Sea	600	-	-	Gulland (1967, 1970)
Inshore North Sea	1 040 - 1 270	-	-	Steele (1956)
English Channel	1 350	-	-	Harvey (1950)
English Channel	550 - 910	-	-	Steele (1956)
Fladen	540 - 820	-	-	Steele (1956)

foraging seabirds from Foula, would lie between 2.82 and 5.64 x 10^{10} kcals yr^{-1}. Taking the lower limit of the seabird community energy requirement of 0.6 x 10^{10} kcals, and the upper limit of 5.64 x 10^{10} kcals of fish production, gives a minimum utilisation by seabirds of 10.6% of fish production, while taking the upper limit of the seabird community energy requirement of 1.8 x 10^{10} kcals, and the lower limit of 2.82 x 10^{10} kcals of fish production, gives a maximum utilisation of 63.8% of fish production. The best estimate, using the mean values of 1.2 x 10^{10} kcals required from 4.2 x 10^{10} kcals produced, suggests that the seabirds utilise 28.6% of fish production, a value slightly greater than the 22% of fish production estimated to be taken by the seabirds of Oregon by Wiens & Scott (1975).

Field and laboratory studies to refine the values of critical parameters will allow this model to be used, together with Monte Carlo determinations of output variances, to analyse in detail the patterns of energy flow through the upper trophic levels of marine systems involving seabirds. With the current rapid increase in the industrial fisheries of Europe, such an analysis would be timely, as industrial fisheries are based on exactly the same fish species as are taken by seabirds. Fisheries studies have indicated that 50% of pelagic fish production in the North Sea area is caught by man (Steele 1974). If seabirds utilise 29% of pelagic fish production, then only 21% remains to be taken by predatory demersal fish species. It is therefore clear that these three energy flows are in competition, so that continued growth of industrial fishing might be expected to reduce food availability to seabirds, resulting in a decline in seabird population sizes.

Of the estimated energy flow to Foula seabirds, totalling 1.235 x 10^{10} kcals yr^{-1}, only 2.68% (3.314 x 10^{8} kcals yr^{-1}) is

utilised by Great Skuas. This puts the Great Skua in sixth place of importance in terms of energy flow in the ranked list (table 44) of the 18 seabird species which reside at Foula for at least part of the year.

The current rapid increase of Great Skua populations in Britain makes it fruitless to search for a constant proportion of energy flow to this species in each community, as might be predicted if the rather similar seabird colony ecosystems were divided into identical niches in each area; results of Operation Seafarer (Cramp et al. 1974) indicate that Great Skuas at the present form a varying, but always small, proportion of the seabird biomass in each Shetland colony. Of greater importance is the trophic position of the Great Skua in the seabird community. Petrels and Shearwaters are considered to obtain a large proportion of their energy from zooplankton. Kittiwakes also take a proportion of zooplankton together with food-fish (principally Ammodytes sp.), while most of the other seabirds feed almost exclusively on food-fish, at least during the breeding season (Witherby et al. 1944) Previous accounts have described the Great Skua as falling anywhere between a top predator, feeding mainly on other seabirds; a pirate, feeding mainly by stealing fish from other seabirds; a surface-feeding seabird, plunge diving on surface shoals of fish (Bannerman 1963, Baxter & Rintoul 1953, Bayes et al. 1964, Burton 1970, Cramp et al. 1974, Meinertzhagen 1959, Venables & Venables 1955, Witherby et al. 1944). The Great Skua utilises all these techniques, together with a small amount of scavenging, for carrion on land and on the sea, and occasional herbivory. If predation on birds and kleptoparasitism of other seabirds are the main feeding methods of the species, then clearly the small energy demand of the species will be of importance in influencing seabird community structure, as it would represent a

large proportion of the production of the community, and would require considerations of predator-prey interactions. If these are but minor feeding methods, then the Great Skua must be considered in competition with the other species taking food-fish, the production of which appears to be a determinant of seabird community size.

Food and feeding studies: methods

No quantitative study of the food of the Great Skua has previously been undertaken. Detailed qualitative or semi-quantitative studies have been published by Bayes et al. (1964), Lockie (1952), Albon et al. (1976), Jackson (1966), and Brathay Exploration Group (Mawby 1969, 1970, 1971, 1973; Furness 1973b, 1974a, b, 1976, 1977a; Burton & Steventon 1971; Collier & Stott 1976). Colonies in Iceland, Faroe and Shetland were included in these studies, but each covered only part of the breeding season, and no attempts were made to convert the observations into quantitative measurements. The wide range of items in the diet of this species is shown in table 46. This list is not complete, as many items of little importance have probably not been recorded in the literature, but it includes all the main items in the diet of North Atlantic Great Skuas during the breeding season. To add to this semi-quantitative list, the following studies were carried out;

1. Exhaustive collections of regurgitated pellets of indigestible food remains were made through the 1975 and 1976 breeding seasons in areas occupied by nonbreeding birds, and from breeding territories on Foula. Rates of pellet decomposition and the amount of food represented by one pellet of each type were determined to allow a quantitative description of the food spectrum through the breeding season. Sizes of otoliths in pellets were used to examine the size range of fish taken

Table 46. A qualitative description of the diet of Great Skuas. Where possible the frequency of different items has been indicated, within categories, and the frequency of each category has been estimated.

Food category	Food item	Estimated Frequency	Locality	Source
PLANT MATERIAL:		RARE		
	Empetrum nigrum berries		Foula	1.
MARINE INVERTIBRATES:		OCCASIONAL		
	Annelida	1% gut	Britain	11.
	Crustacea	4% gut	Britain	11.
	Mollusca (all)	4% gut	Britain	11.
	"Squids"	rare	Iceland	2.
	Mytilus edulis	very rare	Foula	1.
	Lepas sp.	occasional	Foula	1.
TERRESTRIAL INVERTEBRATES:		RARE		
	Tipula sp. larvae	rare	Faeroe	8.
	Mamestra pisi larvae	rare	Faeroe	8.

Table 46. A qualitative description of the diet of Great Skuas. - Continued.

Food category	Food item	Estimated frequency	Locality	Source
FISH		DOMINANT		
	"food fish"	82% gut	Britain	11.
	Ammodytes sp. (marinus?)	staple item	Iceland	6.
		staple item	Faeroe	8.
		staple item	Britain	1, 18, 25.
	Trisopterus esmarkii	frequent	Foula	1.
	Melanogrammus aeglefinus	frequent	Foula	1.
	Merlangius merlangus	frequent	Foula	1.
	Sebastes marinus	rare	Foula	1.
	Micromesistius poutassou	very rare	Foula	1.
	Pleuronectes platessa	very rare	Foula	1.
KLEPTOPARASITISM FROM SEABIRDS	Puffin, Guillemot, Razorbill, Gannet, Herring Gull, Great Black-backed Gull, Kittiwake, Arctic Skua.	OCCASIONAL OR FREQUENT		
MAMMALS:		OCCASIONAL		
	Rabbit	occasional	Shetland	1, 24, 25.
		rare	Orkney	33.

Table 46. A qualitative description of the diet of Great Skuas. - Continued.

Food category	Food item	Estimated frequency	Locality	Source
MAMMALS - Continued	Blue Hare	rare	Faroe	8.
		rare	Orkney	33.
	Hedgehog	rare	Foula	1, 25, 27.
BIRDS EGGS:		OCCASIONAL		
	Kittiwake	frequent	Faroe	8.
		occasional	Hermaness	24.
	Great Skua	frequent	Foula	1, 30.
		rare	Noss	18.
	Guillemot	frequent	Faroe	8, 9.
		occasional	Hermaness	24.
	Fulmar	occasional	Faroe	8, 9.
		occasional	Foula	1, 30.
	Shag	rare	Foula	1.
	Herring Gull	occasional	Hermaness	21.
	Red-throated Diver	occasional	Hermaness	21.
		occasional	Foula	1, 31, 32.
	Eider	rare	Foula	1.
	Oystercatcher	rare	Faroe	8.
		rare	Foula	1.
	Gannet	rare	Hermaness	24.

Table 46. A qualitative description of the diet of Great Skuas. - Continued.

Food category	Food item	Estimated frequency	Locality	Source
BIRDS EGGS, continued	Arctic Tern	rare	Hermaness	24.
	Whimbrel	rare	Faroe	8, 9.
	Razorbill	very rare	Hermaness	24.
	Puffin	very rare	Hermaness	24.
BIRDS:		OCCASIONAL OR COMMON		
	"bird remains"	7% of gut	Britain	11.
	domestic chickens	very rare	Shetland	10.
	domestic ducks	very rare	Shetland	10.
	domestic geese	very rare	Shetland	10.
	Red-throated Diver (chick)	rare	Iceland	6, 7.
		rare	Foula	1, 29, 31.
	Slavonian Grebe (adult)	very rare	Iceland	2.
	Fulmar (adult)	occasional	Iceland	2.
		occasional	Faroe	9.
		occasional	Foula	1, 25, 26.
	(chick)	occasional	Iceland	2.
		occasional	Faroe	8, 9.
	Sooty Shearwater (adult)	very rare	Shetland	12.
	Manx Shearwater (adult)	very rare	Foula	1, 28.

Table 46. A qualitative description of the diet of Great Skuas. - Continued.

Food category	Food item	Estimated frequency	Locality	Source
BIRDS, Continued	Storm Petrel (adult)	occasional	Foula	1, 25, 26.
		rare	Hermaness	24.
	Gannet (adult)	very rare	Hermaness	24.
		very rare	Foula	27.
	(chick)	rare	Hermaness	15.
		rare	Noss	16.
	Shag (adult)	rare	Faroe	8.
		rare	Foula	1, 30.
	Grey Heron (adult)	very rare	Shetland	14.
	Grey-lag Goose (adult)	rare	Iceland	4, 6, 7.
	(chick)	occasional	Iceland	7.
	Shelduck (adult)	very rare	Orkney	13, 17.
	Mallard (adult)	occasional	Iceland	2.
		rare	Foula	27.
	Teal (adult)	occasional	Iceland	2.
		rare	Foula	1.
	Wigeon (adult)	occasional	Iceland	2.
	Scaup (adult)	occasional	Iceland	2.
	Eider (adult)	occasional	Iceland	2.
		occasional	Shetland	1, 12, 16.
		occasional	Orkney	17.

Table 46. A qualitative description of the diet of Great Skuas. - Continued.

Food category	Food item	Estimated Frequency	Locality	Source
BIRDS, continued	Eider (chick)	occasional frequent	Iceland Shetland	6, 7. 1, 16, 32.
	Common Scoter (adult)	occasional rare	Iceland Orkney	2. 17.
	Long-tailed Duck (adult)	occasional rare	Iceland Orkney	2. 17.
	Red-breasted Merganser (adult)	rare	Iceland	2.
	Coot (adult)	very rare	Shetland	10.
	Oystercatcher (adult)	occasional rare	Iceland Shetland	7. 1, 12, 25.
	(fledgling)	occasional	Shetland	1, 19.
	Ringed Plover (adult)	very rare	Foula	27.
	Golden Plover (fledgling)	rare	Iceland	7.
	Lapwing (fledgling)	rare	Foula	25.
	Turnstone (adult)	very rare	Foula	28.
	Dunlin (adult)	very rare	Hermaness	24.
	Curlew (adult)	very rare	Foula	29.
	Whimbrel (adult)	very rare	Shetland	10.
	Snipe (adult)	rare	Shetland	24, 28.

Table 46. A qualitative description of the diet of Great Skuas. - Continued.

Food category	Food item	Estimated frequency	Locality	Source
BIRDS, Continued	Great Skua (chick)	frequent	Faroe	8.
		occasional	Hermaness	15.
		occasional	Foula	1, 30, 32.
		rare	Iceland	7.
	(fledgling)	frequent	Foula	1, 30, 32.
		rare	Fair Isle	19.
		rare	Hermaness	15, 24.
	Arctic Skua (adult)	rare	Faroe	8.
		rare	Foula	1, 25, 34.
	(chick)	occasional	Iceland	3.
		occasional	Faroe	8.
		frequent	Hermaness	15, 24.
		frequent	Foula	1, 22, 34.
	Lesser Black-backed Gull (adult)	rare	Faroe	8.
		rare	Foula	26.
	Herring Gull (adult)	occasional	Shetland	1, 12, 25.
	(chick)	occasional	Hermaness	15.
	Great Black-backed Gull (adult)	occasional	Iceland	4.
		rare	Shetland	26.
		rare	Orkney	13.
	(immature)	occasional	Iceland	5.
	(chick)	frequent	Iceland	3, 4, 7.
	Common Gull (adult)	rare	Foula	27.

Table 46. A qualitative description of the diet of Great Skuas. - Continued.

Food category	Food item	Estimated frequency	Locality	Source
BIRDS, Continued.	Kittiwake (adult)	frequent	Faroe	8, 9.
		frequent	Shetland	15, 30, 32.
	(chick)	frequent	Faroe	8.
		frequent	Hermaness	15, 23.
		rare	Iceland	6.
	(fledgling)	frequent	Faroe	8.
		frequent	Foula	1, 25, 30.
		occasional	Hermaness	15, 23, 24.
	Arctic Tern (adult)	occasional	Iceland	6.
		occasional	Faroe	8.
		occasional	Shetland	12.
		rare	Foula	1, 25, 26.
	(chick)	occasional	Shetland	16.
		very rare	Foula	1.
	Razorbill (adult)	occasional	Iceland	6.
		rare	Hermaness	24.
		rare	Foula	1.
	(fledgling)	occasional	Shetland	22.
	Guillemot (adult)	occasional	Iceland	7.
		occasional	Faroe	8, 9.
		occasional	Shetland	1, 24, 31.
	(fledgling)	frequent	Faroe	8.
		frequent	Iceland	2.
		frequent	Shetland	1, 12.

Table 46. A qualitative description of the diet of Great Skuas - Continued.

Food category	Food item	Estimated frequency	Locality	Source.
BIRDS, Continued	Black Guillemot (adult)	occasional	Foula	1, 25, 30.
	Puffin (adult)	frequent	Iceland	6, 7.
		frequent	Faroe	8, 9.
		frequent	Shetland	1, 18, 24.
	(fledgling)	frequent	Shetland	1, 30.
	Rock Dove (adult)	very rare	Foula	26.
	Feral (Racing) pigeon (adult)	rare	Foula	1, 29, 30.
	Cuckoo (adult)	rare	Shetland	16.
	Skylark (adult)	rare	Foula	28, 29.
	Meadow Pipit (adult)	rare	Foula	27, 31.
	Wheatear (adult)	very rare	Foula	27.
	Crossbill (adult)	very rare	Foula	29.
	Starling (adult)	rare	Foula	26, 27, 30.
CARRION:		OCCASIONAL		
	Gutting offal from boats	occasional	Iceland	2.
		occasional	Faroe	8.
		occasional	Britain	1, 10, 12.
	Grey seal carcass	rare	Iceland	6.
	stranded fish on shoreline	rare	Britain	10.

Table 46. A qualitative description of the diet of Great Skuas - Continued.

Food category	Food item	Estimated frequency	Locality	Source.
CARRION, continued.	Fishing bait on long lines	rare	Hermaness	15.
	Lambs (stillborn or carrion)	occasional	Faroe	8.
		occasional	Shetland	30, 35.
	Gannet chick which fell out nest	rare	Hermaness	23.
	Kittiwake chick fallen out of nest	occasional	Foula	36.
	Domestic rubbish	rare	Shetland	1.

References quoted in table:

1. this study
2. Gudmundsson (1954)
3. Brathay (1967)
4. Brathay (1968)
5. Brathay (1969)
6. Burton & Steventon (1971)
7. Collier & Stott (1976)
8. Bayes et al. (1964)
9. Joensen (1963)
10. Witherby et al. (1941)
11. Collinge (1925)
12. Venables & Venables (1955)
13. Ingram (1949)
14. Campbell & Denzey (1954)
15. Lockie (1952)
16. Meinertzhagen (1941)
17. Meinertzhagen (1959)
18. Perry (1948)
19. Williamson (1957)
20. Fisher & Lockley (1954)
21. Pitt (1922)
22. Pennie (1948)
23. Andersson (1976)
24. Albon et al. (1976)
25. Jackson (1966)
26. Mawby (1969)
27. Mawby (1970)
28. Mawby (1972)
29. Mawby (1973)
30. Furness (1974a)
31. Furness (1976)
32. Furness (1977a)
33. Booth (1976)
34. Furness (1977b)
35. Furness (1977c)
36. Furness, B.L. (1976)

by Great Skuas.

2. Semi-quantitative recording of predation on birds by counting bird corpses on Foula which appeared to have been killed and eaten by Great Skuas was continued to compare with results obtained from pellet analysis.

3. Regular spot observations of the number of birds in their territories through the breeding season were made to examine both seasonal changes and irregular fluctuations in the amount of time spent away from the territory, presumably foraging, and this was compared with changes of food spectrum to infer preferred foods.

4. Regular observation of kleptoparasitic chases by skuas was undertaken to discover the importance of this feeding technique to the species, and its impact on other species.

5. Chick growth data were analysed to allow an independent inference of food availability through the chick-rearing period.

6. Food regurgitated by chicks or dropped by adults was examined to support the pellet study.

7. The effects of weather conditions on food availability were examined by comparing field observations from these studies with weather conditions I recorded on Foula and with data for Lerwick Meteorological Observatory.

Regurgitated pellets

Great Skua scats were collected and examined. None of these contained bones, feathers or otoliths, suggesting that all indigestible material is regurgitated in pellet form by this species. In contrast, Great Blackbacked Gull scats frequently contain numbers of small otoliths of Ammodytes, which must pass through their digestive system. Neither species showed appreciable digestion of otoliths; it has been

assumed that every otolith ingested by adult Great Skuas will be regurgitated in pellets. Chicks do not usually regurgitate pellets, although they swallow entire sandeels, so presumably digest bones and otoliths to obtain the calcium required for growth.

Durability of pellets was examined in 1975. Freshly regurgitated pellets, identified as such by the wet mucus surface, were marked, and examined daily without being moved from the point where they were regurgitated. The number of days between production and disintegration, or disappearance, was recorded (table 47). Too few pellets of eggshell, Lepas shell or rabbit fur were found to allow a study of these categories; the first two are assumed to behave as sandeel pellets, and the last as feather pellets. Casual observations indicated that breakdown rates did not differ greatly under different weather conditions; fish pellets probably break down faster if dry weather, which removes the binding mucous, is followed by heavy rain and strong wind, but under most conditions variation in breakdown rates can be ignored.

On 23 May 1975 four areas on nonbreeder club sites, and territorial mounds in two areas of breeding colony were cleared of pellets. On subsequent visits the pellets of these areas were collected and identified. Knowing breakdown rates, and assuming uniform daily pellet production rates between collecting dates, the total number of each type produced can be calculated from the numbers collected by the formula;

$$\text{Number regurgitated} = \frac{(\text{number found}) \times (\text{number of days between samples})}{(\text{proportion remaining intact})}$$

The denominator of this equation is tablulated in the third column for each pellet type in table 48.

Table 48. Pellet breakdown rates and derived conversion factors.

Age of pellet	Pellet type								
	sandeel			other fish			bird		
	intact		equation denominator	intact		equation denominator	intact		equation denominator
	number	%		number	%		number	%	
0 - 1	38	100	100	28	100	100	10	100	100
1 - 2	36	95	195	26	93	193	10	100	200
2 - 3	30	79	274	16	57	250	10	100	300
3 - 4	19	50	324	8	29	279	10	100	400
4 - 5	9	24	348	2	7	286	10	100	500
5 - 6	6	16	364	0	0	286	10	100	600
6 - 7	2	5	369	0	0	286	10	100	700
7 - 8	1	3	372	0	0	286	10	100	800
8 - 9	1	3	375	0	0	286	10	100	900
9 - 10	0	0	375	0	0	286	10	100	1000
10 - 11	0	0	375	0	0	286	10	100	1100
11 - 12	0	0	375	0	0	286	9	90	1190
12 - 13	0	0	375	0	0	286	9	90	1280

It would be ideal to determine the food equivalent of one pellet of each type by feeding experiments with an adult in captivity. This was not attempted, so indirect methods have been used. Pellets very rarely contain remains of more than one food type; the only regular mixture is of sandeel and pout remains. The use of otoliths in the study of fish age and growth has recently been reviewed (Blacker 1974); the lengths or weights of fish can be accurately estimated from the length of the sagitta, the large otolith, one of which is situated in each of the sacculi, the main paired chambers of the fish labyrinth. Thus, each fish eaten will result in two otoliths being included in pellets (the lapillus and asteriscus are so small that they are not found in pellets). The species and sizes of the fish eaten can be obtained from study of the otoliths in the pellets. Otoliths of only seven species were found in the thousands of fish pellets collected on Foula. A very small number of Redfish, Blue Whiting and Plaice otoliths were found, with only one, two or three in any pellet, suggesting that each Redfish, Blue Whiting or Plaice pellet comprised remains from one fish. Numbers of otoliths in pellets of sandeel remains (table 48) show that sandeel pellets represent between one and 16 fish, but usually contain about six, the average number of otoliths per pellet containing sandeels being 12.2 $\pm$ 1.0. Norway Pout, Haddock and Whiting pellets contain fewer otoliths (table 49), as would be expected as they are larger fish; the mean number of otoliths per pellet, which does not differ significantly between these species, and averages 1.61 $\pm$ 0.037, suggests that 1.24 pellets of remains are produced for every Norway Pout, Haddock or Whiting (PHW) eaten. Alternatively, some otoliths may be lost because not all fish heads are eaten; this seems unlikely as Great Skuas are easily able to swallow objects with a diameter of up to 5 centimeters, which includes

Table 48. Numbers of otoliths per pellet of sandeel remains.

Number of otoliths	frequency
0 - 2	1
3 - 5	3
6 - 8	14
9 - 11	12
12 - 14	3
15 - 17	6
18 - 20	2
21 - 23	2
24 - 26	1
27 - 29	1
30 - 32	2
Total	47

Table 49. Numbers of otoliths per pellet of Pout, Haddock or Whiting remains.

Number of otoliths	frequency
0	118
1	145
2	404
3	20
4	31
5	2
6	1
7	1
Total	722

all of the fish sizes recorded in the prey spectrum. The preponderance of pellets containing two otoliths, and large number containing four suggest that most otoliths are incorporated into pellets; pellets containing odd numbers or no otoliths are probably the result of the production of two pellets from the remains of one fish. It was also noted that otolith sizes in pellets containing two otoliths were virtually identical in almost every case, and consisted of a right and a left facing otolith which presumably came from the same fish.

Mixed pellets usually contained sandeel bones, scales and otoliths plus Pout, Haddock or Whiting (PHW) otoliths, but with no PHW bones or scales. This, together with the fact that the mean number of otoliths per PHW pellet is 1.6 rather than 2.0, although PHW pellets rarely appear to contain bones of more or less than one complete fish, suggests that PHW otoliths may sometimes remain in the stomach when the bones are regurgitated, and then be regurgitated later in a sandeel pellet. Although based on a small sample, numbers of otoliths of sandeel and PHW in mixed pellets (table 50) do not differ significantly from numbers in single-species pellets; absence of PHW bones suggests that these are normal sandeel pellets with added PHW otoliths remaining from an earlier meal.

Pellets containing eggshell fragments were always single-species, implying that one robbed egg or clutch resulted in the production of one eggshell pellet. Similarly, barnacle pellets were always found to contain nothing but barnacle fragments, representing about three to five complete individuals. Pellets of mammal or bird remains are more difficult to assess; different prey species result in different amounts of waste material. Pellets of Storm Petrels or similarly sized passerines, were found to contain entire remains of one bird; head, legs,

Table 50. Number of otoliths of each species per pellet of mixed fish remains.

Number of sandeel otoliths.		Number of Pout, Haddock or Whiting otoliths.
15	+	2
10	+	1
9	+	2
9	+	1
8	+	1
6	+	6
5	+	2
Mean number of otoliths per pellet: 8.86	+	2.14

wings, body feathers, bones and tail. Pellets of auks, Kittiwakes, etc. usually contain either tail feathers, leg plus body feathers or body feathers alone; wings and heads are not swallowed. Dead birds of this size on the sea are often shared by two or three Great Skuas; kills within a territory may be eaten in several meals or by both adults. These observations suggest that each bird of this size will result in three or four pellets of remains when completely eaten. A rabbit probably results in only one to three pellets, as only fur and small bones occur in pellets, indicating that the corpse is picked clean carefully, whereas, with bird kills, everything except the wings, sternum, head and occasionally legs or tail, will be swallowed. Feeding experiments would be useful to confirm these results, but I am confident that these conversion factors (table 51) are close to the real values.

Table 51. Number of individuals represented by one regurgitated pellet of remains.

Prey Item	Mean number of individuals per pellet
Sandeel	6
Norway Pout, Haddock or Whiting	1
Redfish, Blue Whiting or Plaice	1
Barnacle	4
Eggs	1
Rabbit	0.5
Bird ($<$ 100g)	1
Bird ($>$ 100g)	0.25

In 1976, pellet collections were made in cleared areas every 48 hours. Only 6% of fish pellets disintegrate within 48 hours after regurgitation. Although disintegrated, some of these can still be collected, so the numbers of each type of pellet collected are almost identical to the numbers produced. Pellet collections in 1975 were made at intervals of four to 13 days, so have to be corrected for considerable differential breakdown which occurs.

Diets of breeders, nonbreeders and chicks

Chicks do not produce pellets, but 3.8% of those handled (n = 3827) for ringing or measuring in 1975 regurgitated food. This percentage showed no significant heterogeneity with date or chick age. With only a very small proportion of chicks providing food samples, a considerable bias could result if one food type is more easily regurgitated than another. This would appear not to be the case, as the correlations between the percentage of chicks regurgitating and the percentages of regurgitated samples which were sandeels ($r = +0.16$), PHW ($r = -0.58$) or meat ($r = +0.18$) fall below significance levels, although the high negative coefficient with the percentage of PHW ($r = -0.58$, $df = 6$, $p > 0.1$) suggests that there might be a tendency for PHW to be less easily regurgitated. This is the most likely bias to arise, as Norway Pout, Haddock and Whiting are bulky and rigid, and often chicks have some difficulty in swallowing these species. It is usually impossible to distinguish between these three species from the semidigested material regurgitated by the chicks. As these correlations are not statistically significant, it is assumed that regurgitations are unbiassed samples, so the chick diet may be compared with diets of breeders and nonbreeders determined from corrected pellet type frequencies. Variations in proportions

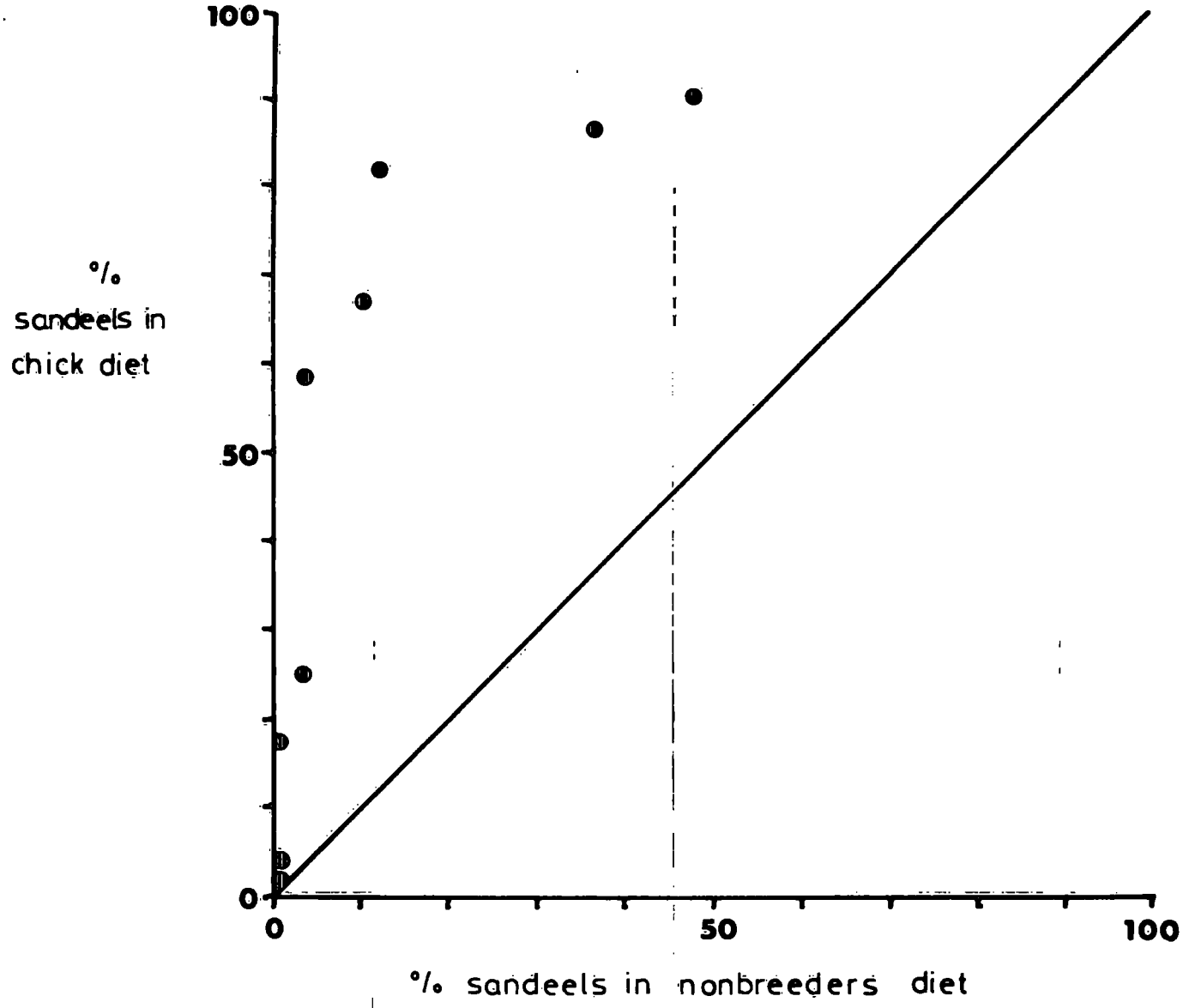
of prey types taken throughout the chick rearing period (1 June to 10 August) in 1975 on Foula are shown in table 52.

Table 52. Percentage frequency of feeds of different types in the diets of chicks, nonbreeders and breeders during the chick rearing period (1 June to 10 August) on Foula in 1975, based on examination 2172 pellets and regurgitated food samples from 146 of 3827 chicks handled.

Age group	Percentage of:			
	sandeels	Norway Pout, Haddock and Whiting	birds and mammals	other items
Chicks	65.8	30.8	3.4	0.0
Breeders	41.8	54.2	2.6	1.4
Nonbreeders	25.9	71.1	1.4	1.6

It is clear that chicks were given a higher proportion of sandeels than eaten by breeders or nonbreeders. The percentage of sandeels in the diets of chicks and nonbreeders over given intervals during the chick rearing period (figure 17) show that the parents continue to feed their chicks almost entirely on sandeels even when these are scarce, and have been abandoned as a primary food source by non-breeders. Possibly sandeels are a better source of a particular requirement of growing chicks, for example calcium, than are Norway Pout, Haddock or Whiting, or they may simply be easier for the chicks to handle or to digest. It is also clear that breeders take more sandeels than nonbreeders, even after they have fed their chicks principally on sandeels. This was shown both during the chick rearing period in

Figure 17. The relationship between the percentage of sandeels in the diets of nonbreeders and chicks between June and August 1975 on Foula. The diagonal line is the expected relationship if sandeels were equally preferred by nonbreeders and chicks. There is a clear tendency for chicks to be given a higher proportion of sandeels than is taken by nonbreeders, particularly when sandeels are scarce.


100
50
0
0
50
100
% sandeels in chick diet
% sandeels in nonbreeders diet

1975 (figure 18), when breeders consistently took 15% more sandeels than nonbreeders over a range of 0 to 60% sandeels in the diet, and in 1976 in May and early June, before there were any chicks to be fed, when breeders consistently took 15% more sandeels than non-breeders over a range of 60 to 100% sandeels in the diet (figure 19). These differences, while pronounced, are small compared to the differences which may occur between years (table 53).

Variation in diet also occurs between colonies, but this is consistent from year to year and involves the minor items in the food spectrum. It is clear that certain feeding techniques have developed in some colonies but not in others, and these presumably spread within colonies by imitative learning (Cushing 1944). Thus, for example, on Foula, Great Skuas kill large numbers of fledgling Kittiwakes but never take eggs or chicks from Kittiwake nests; on Hermaness they take both eggs and chicks from nests, but rarely, if ever, kill fledglings (table 54). The establishment of such traditional feeding behaviour has been seen by Gudmundsson (in litt.) who noted the spread of the habit of killing adult Fulmars. This habit was unknown in Iceland before the war, then slowly spread from one site in south Iceland. It now occurs in several localised areas, but is confined to a small number of individual birds (Burton & Steventon 1971, Collier & Stott 1976). On Foula there has been a similar growth, of Shag killing, which is presently confined to a very small part of the colony, but was unknown before 1970 (Mawby 1970), although pellets containing Shag feathers are particularly easy to identify. These traditions presumably arise from chance learning by one individual of a particular feeding technique or application of an established method. The Great Skua can be a very adaptable and opportunistic feeder; one individual may catch Puffins in flight over the sea, another may stand

Figures 18 and 19. ABOVE: Relationship between the percentage of sandeels in the diets of breeders and nonbreeders on Foula in 1975.

BELOW: Relationship between the percentages of sandeels in the diets of breeders and nonbreeders on Foula in 1976.

There is a clear tendency for breeders to take a higher proportion of sandeels than taken by nonbreeders, both in a season of low sandeel availability (1975) and in a season of high sandeel availability (1976).

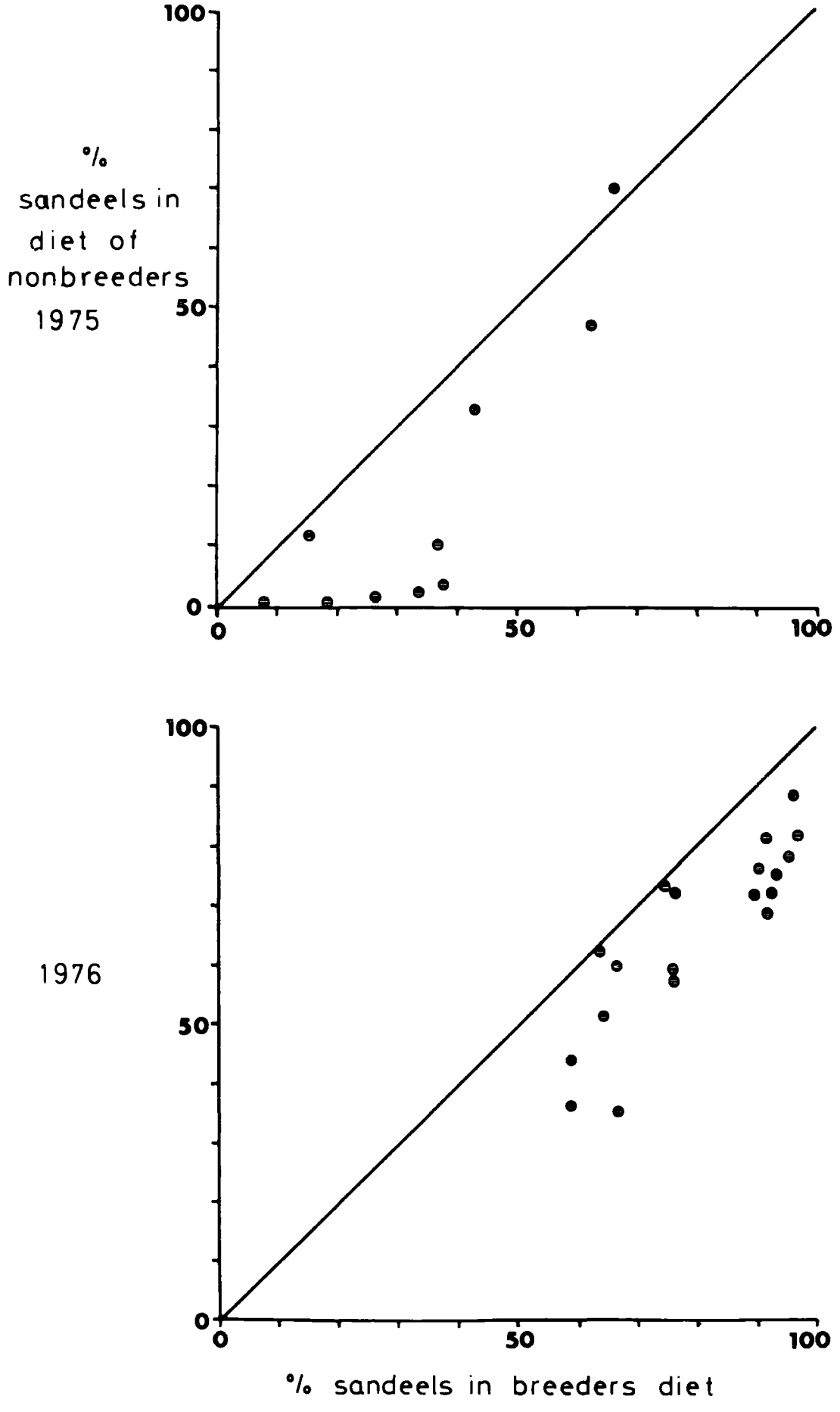

%
sandeels in
diet of
nonbreeders
1975
100
50
0
0
50
100
1976
100
50
0
0
50
100
% sandeels in breeders diet

Table 53. Percentages of different food, identified from pellets, in the diets of nonbreeders in successive years (during the chick rearing period only i.e. 1 June to 10 August).

Year	corrected total of pellets	food item: sandeel	Norway Pout	Haddock	Whiting	other fish	bird or mammal	other items
1975	5317	25.9	17.6	27.1	25.9	0.5	1.4	1.6
1976	1536	67.9	4.6	9.4	15.2	0.6	0.7	1.6

Table 54. A comparison of prey spectra in those colonies examined in some detail, showing items which indicate traditional differences in diets of different Great Skua colonies.

Prey item	Colony:				
	Foula	Noss	Hermaness	Faroe	Iceland
Food-fish	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX
Mammals	X	.	X	X	.
Kittiwake					
adults	X	XX	XX	XX	X
fledglings	XXXX	X	.	XX	XX
nestlings	.	X	XX	XX	.
eggs	.	X	X	XX	.
Great Skua					
fledglings	XXXX	.	X	.	.
nestlings	X	X	X	XX	X
eggs	XX	X	.	X	.
Arctic Skua					
chicks	XXX	X	XX	XX	X
Arctic Tern					
adults	X	.	X	X	X
chicks	.	X	.	.	.
eggs	.	.	X	.	.
Black Guillemot					
adult	XX	.	.	.	.

Key:

. not recorded as a prey item
X rare
XX occasional
XXX regular
XXXX frequent
XXXXX principal item of diet

Sources: Foula: 1969 - 1976 (this study); Noss: Perry (1948); Hermaness: Lockie (1952), Albon et al. (1976), Andersson (1976); Faroe: Joensen (1963), Bayes et al. (1964); Iceland: Brathay 1967 - 1976.

over the burrow and pounce on an emerging bird, another may reach down into the entrance, yet another may hover over a diving Puffin until it tires and can be lifted off the sea.

While there are clear differences in feeding methods and diets of individuals, there is also a very clear tendency for birds in particular parts of the Foula colony to feed on locally available items; where there are Arctic Skuas nesting nearby, individuals are more likely to specialise in killing Arctic Skua chicks than adult Puffins, and the reverse is also true. Comparison of the bird pellets found in territories in Lochs and Flick areas of the Foula colony during the chick-rearing period in 1975 (table 55) shows that there is significant overall heterogeneity, (X^2 = 22.71, df = 5, $p < 0.005$) with greater numbers of pellets of Kittiwakes and Shags in Loch territories and more Auk pellets in Flick territories, reflecting the breeding distributions of these prey species around Foula. Although the birds in adjacent territories may specialise in different species (Furness 1974a), the distribution of killed birds tends to closely reflect the distribution of prey species around the island (Furness 1973b, 1974a). The very local nature of this predation suggests that it may be almost entirely due to the on-duty member of breeding pairs which may take occasional opportunities to kill birds or mammals within or close to the territory. Belopolskii (1961) showed considerable differences in diet between male and female breeding seabirds of many species by analysing stomach contents of shot samples. I was unable to study dietary differences between the sexes as I did not wish to shoot birds, but observations of daily activity patterns of breeding pairs, and spot observations of attendance of known birds, showed clear sexual differentiation of behaviour throughout the breeding season (Furness 1976, 1977a). In general, females remain on the territory while males forage,

Table 55. Numbers of pellets of bird remains at two parts of the Foula colony in 1975.

Species	Flick		Loch	
	number	%	number	%
Auk	22	69	12	24
Kittiwake	7	22	14	29
Great Skua	3	9	3	6
Shag	0	0	16	33
Fulmar	0	0	3	6
Storm Petrel	0	0	1	2

providing food for the female and the chicks. However, females make short sorties to feed when the chicks are well grown, and are also opportunistic killers of occasional birds and mammals which enter their territory (Furness 1977c). Thus most predation of birds during the incubation or chick rearing period can probably be ascribed to breeding females on territories. Nonbreeders also kill birds and mammals, but less frequently (table 56), and take different species; nonbreeders on the club sites in the Lochs area took larger numbers of Storm Petrels and Auks than did breeders in the same area (table 56) ($X^2 = 12.9$, df = 5, $p < 0.05$). These two species are probably killed at sea by nonbreeders, or may be obtained as carrion at sea. Most of the birds taken by breeders were probably killed at Foula.

Comparison of the diet of breeders and nonbreeders through the breeding season by X^2 analysis for heterogeneity of pellet types between groups indicates that differences occur, but these alter through the season. Breeders take a higher proportion of birds than nonbreeders in May, but in July and August the reverse is true ($X^2 = 22.99$, df = 4, $p < 0.005$). Breeders take more eggs than non-breeders, but fewer barnacles or mussels ($X^2 = 9.86$, df = 1, $p < 0.005$). This is also indicative of the opportunistic feeding of on duty breeders, principally females, within their territories, and of non-breeders during their prolonged foraging periods spent each day at sea (see later). During the pre-laying period breeders spend longer in foraging, and they then take larger numbers of barnacles, presumably picked off drifting wood, but still take fewer than nonbreeders. In the first ten days of May 1976, three of 126 (2.4%) of breeders pellets were of barnacles compared to 13 of 181 (7.2%) of nonbreeder pellets in this period. While these differences between breeders and nonbreeders can be easily measured from the large sample of pellets

Table 56. Comparison of the types of bird taken by breeders and nonbreeders from the same part of the Foula colony in 1975.

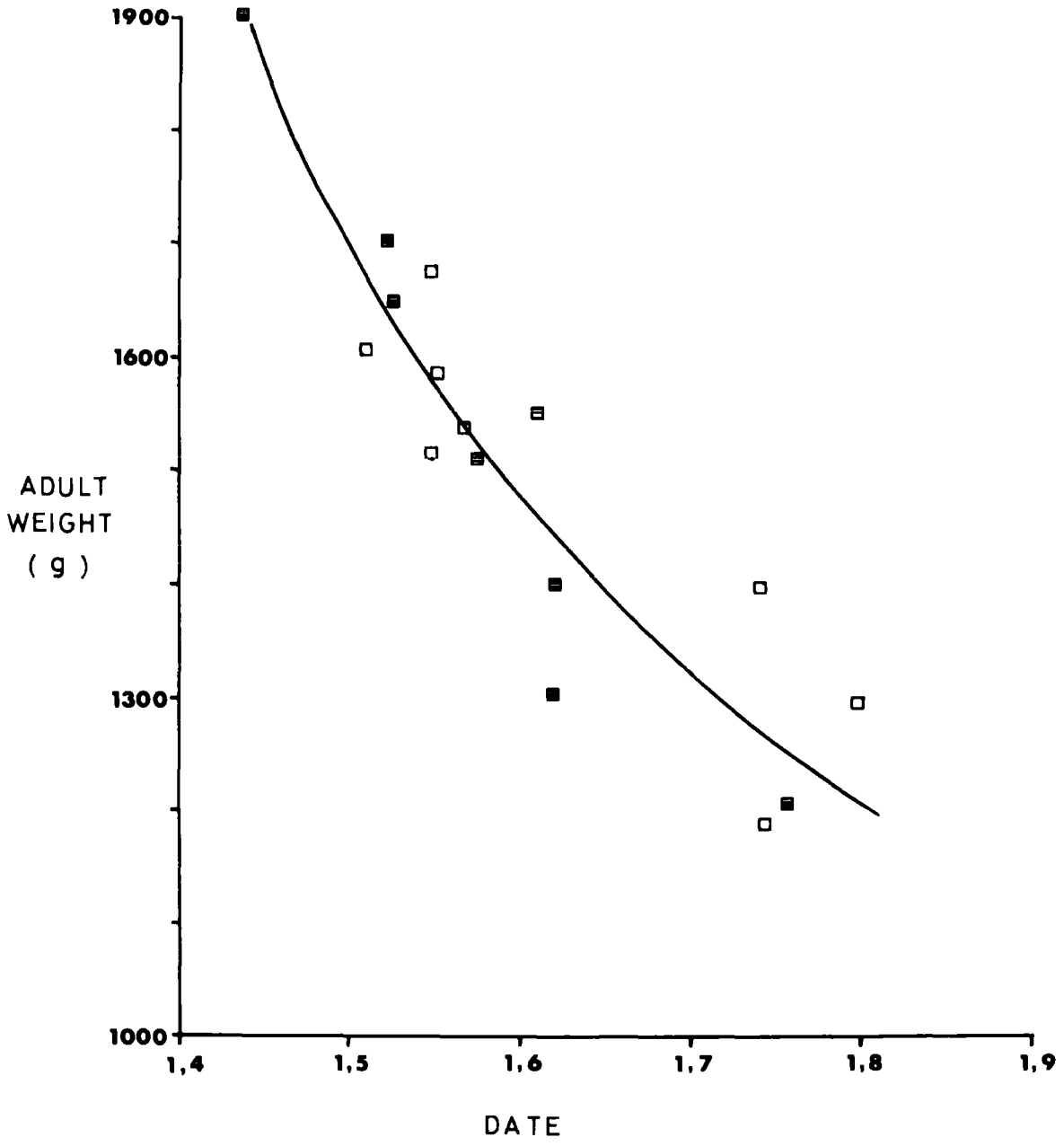
Species	Breeders		Nonbreeders	
	number	%	number	%
Auk	12	24	30	40
Storm Petrel	1	2	5	7
Great Skua	3	6	7	9
Kittiwake	14	29	23	30
Shag	16	33	11	14
Fulmar	3	6	0	0

collected, they are very small differences in terms of the numbers of feeds of each type taken. Feeds of both breeders and nonbreeders comprise fish in more than 95% of cases, but with the proportions of sandeel, Pout, Haddock and Whiting differing slightly between the two groups.

Time budgets of breeders and nonbreeders

At most stages of the breeding season, and at most times of day, both adults can be found on their territory. Superficially, this suggests that they have little trouble in obtaining food. However, adult Great Skuas are very fat when they arrive at Shetland colonies in spring, but they decline in weight through the breeding season (figure 20). This decline may not be associated with stresses of breeding, as both breeders and nonbreeders follow the same curve, but it suggests that there could be other breeding season activities of greater importance than the maintenance of high body weight, and fat reserves may be important in allowing birds to devote as much time as possible to these. To examine the seasonal changes in the amount of time spent by breeding birds in foraging, spot observations of the number of birds in each of six territories were made on altermate days between 0800 and 1600 hrs from 6 May to 4 August 1976. On hatching, brood sizes of the study pairs were manipulated to give one brood of four hatching chicks, one of three, two of two and two of one chick. It was impossible to ensure that pairs with identical laying dates were compared, but the pairs that were chosen all hatched the eggs within a three-week period, and hatching order was not significantly related to the manipulated brood size. All artificial broods were accepted by the adults, and all the chicks survived to the end of the study period. As might be expected, there was no significant variation

Figure 20. Weights of adult Great Skuas on Foula through the breeding season. Most weights were taken in 1976, with a few from 1974 and 1975. There was no evidence of differences between the three seasons, or between sexes. Breeding birds are marked ■ and prebreeders are marked □ . These two groups seem to follow the same curve, suggesting that weight loss is not due to stresses of breeding.


1900
1600
1300
1000
ADULT
WEIGHT
(g)
1,4
1,5
1,6
1,7
1,8
1,9
DATE

between pairs in the number of adults counted in the territory on dates before hatching ($X^2 = 0.92$, df = 3, $p > 0.5$). During the first 14 days of chick rearing, from 21 June to 5 July, there was no significant variation in the number of adults counted in relation to the manipulated brood size ($X^2 = 1.64$, df = 2, $p > 0.1$) although the differences were in the expected direction; i.e. birds with larger broods were recorded less often in their territory. Between 5 July and 4 August the chicks grew rapidly to fledging age and then independence, and their food demands were therefore greatest during this period. Over these dates, the average number of birds counted, which is a measure of the average amount of time spent at the territory per bird, varied in relation to the number of chicks being reared (table 57).

Although the mean number of birds present varied considerably between the two pairs with only one chick, and also between the two pairs with two chicks, these differences are not significant ($0.1 > p > 0.05$ in both cases) but each difference between brood sizes is significant ($p < 0.01$ in every case). Assuming a feeding daylength of 20 hours as indicated by the 24 hour hide studies (see below) the attendance of 1.367 adults per observation of broods with two chicks would indicate that, on average, 760 minutes were spent away from the territory during July days. This is in close agreement with the results of the hide studies. A further observation is that rearing broods of more than two chicks necessitates both parents leaving the territory unguarded on occasions (mean number on territory ≤ 1.0), while, with efficient coordination, parents of broods of two chicks could spend the required time away without both birds ever being away simultaneously. This effect of brood size could be of importance in determining breeding success as chick predation by

Table 57. Mean amount of time spent away from the territory during the second half of the chick rearing period in relation to brood size, derived from spot observations of the number of adults in each of six territories on Foula in 1976 (dates between 5 July and 4 August).

Brood size	Number adults in territory			Total minutes away from territory assuming feeding day from 0330-2330 hrs.
	mean	SE.	95% confidence interval	
4	0.667	0.025	0.615 - 0.719	1600
3	1.000	0.019	0.960 - 1.040	1200
2	1.333	0.016	1.299 - 1.367	760
	1.400	0.017	1.364 - 1.436	
1	1.533	0.018	1.495 - 1.571	520
	1.600	0.017	1.564 - 1.636	

other Great Skuas is a major cause of loss in the Foula colony.

With the help of members of Brathay expeditions, one pair of Great Skuas with a brood of two chicks was watched from a hide on five dates between 16 and 31 July 1974. The male was eight years old and had been ringed as a chick on Foula in 1966. He was almost certainly breeding for the first time but had not been seen holding territory in this area in previous seasons. The female was unringed (sex was determined by observation of behaviour and size difference). They hatched two chicks; one on 7 July and the second on 8 July. Watches were maintained from a hide and the activities of the adults and chicks were recorded. The earliest feeding departure recorded was at 0330 hrs and the latest return after a period away from the territory was at 2330 hrs. Both birds remained on the territory through the night. On 16 July, when the chicks were aged 8 and 9 days, the parents took turns in brooding both chicks between midnight and 1500 hrs. The amount of time spent away from the territory is shown in table 58. This pair was unusual in that they nested near a cliff edge. This allowed them to chase juvenile Kittiwakes passing along the clifftop. Most of the departures of the female were to assist her mate in attacking Kittiwakes, or to eat a kill. The small number of prolonged departures by the female can be seen from table 59. The male did most of the foraging, particularly during the early part of the chick rearing period. The increasing amount of time spent away by the female appears to be due to the inability of the male, perhaps through inexperience as well as food shortage, to obtain sufficient food for the family. This is indicated by the total number of regurgitations made in each period and by the total number of feeds by each chick (table 60). Not all regurgitations resulted in chicks being fed. On several occasions the female swallowed the food

Table 58. Time spent away from the territory by a pair watched over five 24 hour periods in 1974, (minutes).

Bird	Date				
	16 July	19 July	21 July	26 July	31 July
Male away	540	503	380	488	684
Female away	38	79	150	164	282
Total time	578	582	530	652	966
Both away	0	45	50	65	240

Table 59. Number of feeding departures (longer than 10 minutes).

Bird	Date				
	16 July	19 July	21 July	26 July	31 July
Male	14	16	10	9	12
Female	1	2	4	6	9

Table 60. Number of regurgitations by each parent and the number of Feeds by each chick.

Category	Date				
	16 July	19 July	21 July	26 July	31 July
Regurgitations;					
Male	11	11	11	4	4
Female	4	3	6	3	2
Feeds; chick 1	9	5	2	0	0
chick 2	11	8	5	3	2

regurgitated by the male. The inability of the first-hatched chick to obtain sufficient food resulted in its starvation and death on 31 July. The second chick subsequently fledged. On 16 and 19 July, the male spent 10 times as long away from the territory as the female, and she obtained food by begging from him when he returned to the territory. By 31 July, the female had increased her foraging activity to nearly one half that of the male, and the territory was left unguarded for considerable periods. Spot observations of other pairs in which both adults were individually colour ringed and of known sex, showed that females remain in the territory almost continuously throughout the incubation and chick rearing period, and they appear to be fed regularly by the male. A similar, but less pronounced division of labour occurs in the Arctic Skua (Furness 1977a) and in the South Polar Skua (Young 1963).

One 24 hour watch of a different pair, with both of the adults individually colour ringed and of known sex, was carried out on 18 July 1976 to compare with the 1974 study. As in the previous watches, there was a clear sexual dimorphism in behaviour. The male spent much more time foraging, and his trips were longer (table 61). At no time were both birds away from the territory (table 62), and both birds remained on the territory through the hours of darkness.

Great Skuas appear not to become active until well after first light. In this watch the male did not set off to feed until 0542, and this was typical of adjacent pairs also. In contrast, Arctic Skuas began foraging before 0430 in each of three territories watched on Foula over 24 hour periods in 1976 (Furness 1977a). Because the first feeding trip may last for more than an hour, the chicks are not usually fed until 0600 or later, but feeding trips occurred throughout the daylight period, showing no pattern other than that caused by the

Table 61. Feeding trips by members of a marked pair in 1976.

Trips by the male		Trips by the female	
Time away	Duration (minutes)	Time away	Duration (minutes)
0542 - 1013	271	1125 - 1157	32
1037 - 1122	45	1326 - 1345	19
1200 - 1222	22	2207 - 2219	12
1235 - 1253	18		
1314 - 1328	14		
1353 - 1540	107		
1650 - 1912	142		
1931 - 1959	28		

Table 62. Time budget for the pair of Great Skuas watched on 18 July 1976.

Time present in territory (minutes)	of 24 hours	of daylight period (total 19 hours)
Both birds together	730	430
Male only	63	63
Female only	647	647
Neither adult present	0	0

inactive period during darkness and the early morning. Apart from foraging, the Great Skuas are very inactive; only a total of 41 bird-minutes were spent in territorial defence, short flights for unknown reasons or flights acress the territory to a different resting point (table 63) by the pair watched in 1976.

Table 63. Periods of flying activity at a territory of Great Skuas watched on 18 July 1976.

Reason for activity	Minutes spent in flight by;		
	both adults	male	female
Chasing intruding Great Skua	0	0	1
Chasing intruding Arctic Skua	3	0	.6
Change of position	0	1	12
Unknown reason	0	5	10

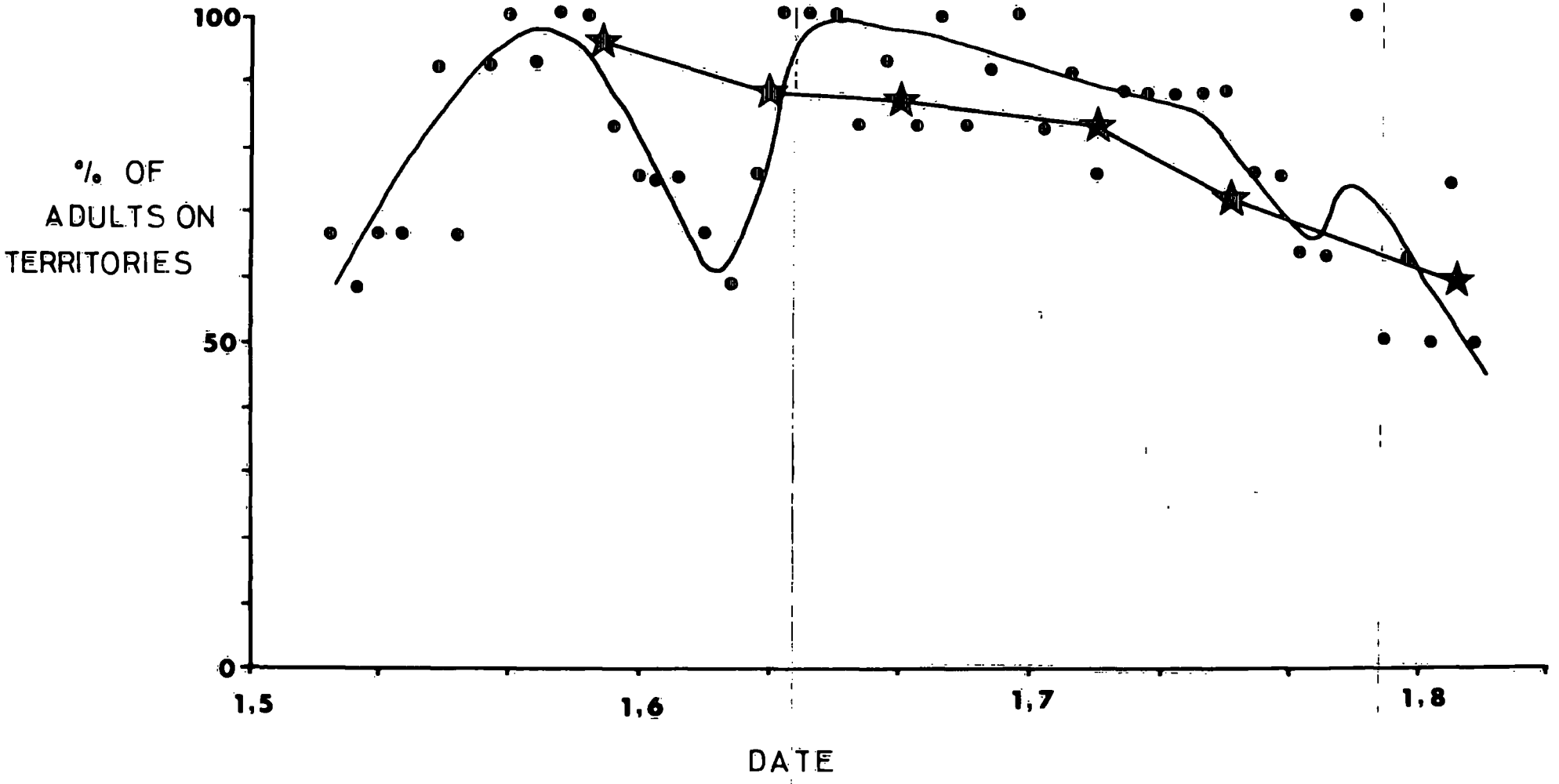
After almost every trip out of the territory, the returning bird regurgitated food. This suggests that all the trips, except perhaps a few of the shortest ones, are to feed. The only other activity in which breeding adults may be indulging is bathing or drinking in freshwater pools. On Foula there are usually about 100 individuals bathing in a large flock on Mill Loch or Overfandal Loch. If these were all breeding birds this would represent 1.7% of the population at any one time, but a large proportion of these are nonbreeders (they can be identified as too young to be breeding by their colour ring combinations) so it seems unlikely that breeders spend as much as 1% of the daylight period bathing.

The relationship between brood size and time spent away from the territory, and the direct 24 hour hide watches indicate that very little time is spent away from the territory in activities other than foraging. Thus, as attendance did not vary between pairs before 5 July, the total number of adults present on the six territories can be used as a measure of food availability. The number of adults counted varied between seven, when it appears that food must have been difficult to obtain, up to 12, on which days food may have been easily obtained in a short space of time. After 5 July, the extra food requirement of chicks became an important factor in determining the amount of time spent away from the territory; only the four pairs with normal brood sizes were used to measure food availability. Sampling error with only 12 or eight birds under observation makes it difficult to infer changes in day to day food availability, but trends over longer periods can be seen (figure 21). Before 5 July, food availability is measured in absolute terms, as the seasonal changes in food requirements of adults are small except during the chick rearing period. After 5 July, food availability is measured only in relation to the food requirement. Because of chick growth, the latter will rise to a peak around 35 days of chick age, equivalent to 15 - 25 July for the study pairs, then fall slightly as chick growth rate declines.

There was a clear improvement in food availability between 1 and 20 May, followed by a sharp reduction in availability over the period 28 May to 10 June, then a rapid improvement, and continuous high availability up to mid-July. Availability then fell rapidly until August, continuing to fall after the peak of chick food requirement had passed.

No direct observations of the duration of foraging trips by

Figure 21. Percentage of adults present on selected territories on Foula through the seasons of 1975 (★) and 1976 (●). This percentage is taken to be an index of food availability (see text).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nonbreeders attending clubs were made. Potts (1961) counted the number of birds on a club in the Faroes through several 24 hour periods, and found that the number present built up from an early morning minimum to a mid-afternoon peak, decreased slightly in the late afternoon, then increased to an overnight peak. He considered that all the nonbreeders remained on the club at night with none staying at sea and returning in the morning. The same pattern was found on Foula (Furness 1974a). Counts of the number present on alternate hours on four dates in 1976 (table 64) show the diurnal pattern. Assuming the highest nocturnal count to represent the total number of non-breeders associated with the club, and assuming that no breeders visit the club (see section 3), the number of birds away from the club can be calculated, and this gives an estimate of the average number of hours per bird spent in foraging activities.

Because club sites are discrete groups of birds, with little movement of birds between clubs, the average amount of time spent away from the club by each nonbreeder can be estimated as 12 times the highest nocturnal count minus the sum of all 12 counts, times 24/12 (hours), divided by the highest nocturnal count. The result is the mean time away in hours. Multiplying by 60 to give the result in minutes; on 25 May it was 407 minutes, on 5 June it was 651 minutes, on 15 June it was 349 minutes and on 15 July it was 579 minutes. On average, nonbreeders spend as long away from their club site as a breeding male with a mate and one chick to feed. Although some of this time may be spent in bathing in Mill Loch or Overfandal Loch, or in attempting to establish a territory in some part of the colony, most must be spent at sea, presumably in foraging. This is also indicated by the differences in the mean amount of time spent away on different dates. These parallel the changes in breeder attendance

Table 64. Counts of the number of nonbreeders on Strem Ness club site on alternate hours on four dates in 1976.

Date	Hour												Sum of Counts
	0200	0400	0600	0800	1000	1200	1400	1600	1800	2000	2200	2400	
25 May	77	76	38	24	48	52	63	50	33	54	72	76	663
5 June	70	68	46	12	20	27	36	30	22	24	38	67	460
15 June	98	98	61	52	59	68	75	70	57	67	89	97	891
15 July	73	69	27	14	20	31	40	32	38	41	66	73	524

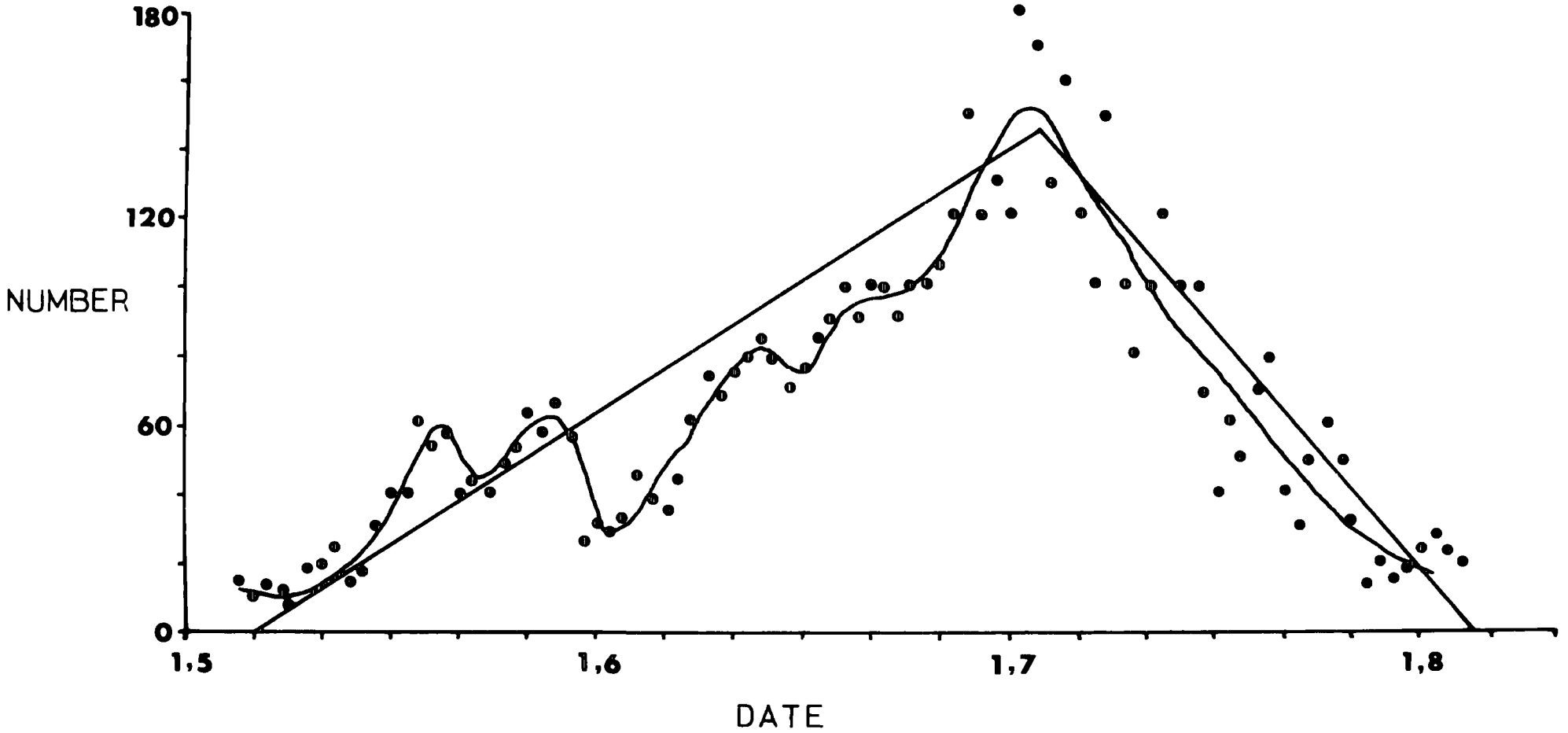
shown by spot observations, again indicating food availability to have been poor in early June and mid-July but good in late May and mid-June.

If food availability variations result in variations in the amount of time nonbreeders spend on the club, then the afternoon peak number of nonbreeders might be a sensitive index of food availability. Daily counts, from 4 May to 2 August 1976, were made of numbers on three of the club sites. Unfortunately, it is difficult to distinguish between seasonal trends in nonbreeder attendance, day to day chance fluctuations in numbers, and effects of food availability. Counts for Strem Ness club (figure 22) are shown as a curve, fitted by eye, which removes the day to day fluctuations. If numbers of nonbreeders are assumed to increase linearly to a peak then decrease linearly from that peak, the difference between the fitted curve and the expected line is a measure of the difficulty of obtaining food. This analysis suggests that food was short in 1976 between 29 May and 7 June in particular, in close agreement with adult breeder attendance pattern analysis (figure 21). Thus, spot observation of breeder attendance, diurnal counts of nonbreeder attendance and daily counts of nonbreeder numbers at the afternoon peak, all indicate a severe food shortage in early June. The first two methods, which are probably more sensitive, also indicate an improvement of food availability before and after this period, and deteriorating food availability during the second half of July.

Food preferences

Assuming that the preferred food of breeding Great Skuas is that which gives the greatest energy gain per unit of foraging time, which is probably the case for breeders, but may not be so important for

Figure 22. Numbers of prebreeders at a Foula club site through the season of 1976. Counts were made daily at the early afternoon peak of attendance. The curve is fitted by eye. The straight line increasing to a peak at the start of July and decreasing to zero in early August is an assumed "expected" trend. Deviations of the curve from this expected are taken to be an indication of food availability (see text).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nonbreeders, the proportions of different pellet types can be compared with the amount of time breeders spend at the territory on alternate days through 1976. These correlations (table 65) indicate that sandeels are the preferred diet as they are the only item to be positively correlated with the amount of time spent on territory. None of the slopes of the regressions show significant differences between the two time periods so there is no indication of a change in preference or of the size of the preference between incubation and chick rearing periods.

PHW, barnacles and mussels appear to be secondary foods, taken when sandeels are not abundantly available. Birds, mammals and birds eggs appear to be taken when the opportunity is presented, but not particularly sought after as alternatives to sandeels or Norway Pout, Haddock or Whiting. These observations fit the concept of territorially resident females killing small numbers of birds, mammals and birds eggs, while males forage to feed the whole family, for short periods on sandeels if available, or for longer periods on Norway Pout, Haddock or Whiting if sandeels are not available, or on barnacles or mussels if these are chanced upon or if all fish are scarce. Norway Pout, Haddock and Whiting are demersal species which could not be caught by Great Skuas. They must be obtained as a result of man's fishing activities. This assumption is confirmed by the sizes of fish of these species taken by Great Skuas, which are almost invariably the sizes rejected by fishermen because they are below the legal limit or are just above the limit but too small to be worth marketing. The rare occurrence of Plaice, Redfish and Blue Whiting in the Great Skua diet also indicates the origin to be from fishing boats as these species are also demersal and available to Great Skuas only as rejects from boats. Although breeding Great Skuas prefer to

Table 65. Regression of the percentage of each prey type in pellet samples on the percentage of birds on their territories at spot observations on alternate days through part of the 1976 breeding season.

Prey type	Date	Sample size	slope	SE slope	intercept	correlation coefficient	probability level
Sandeel	before 7 July	31	0.56	0.14	28.9	+0.588	$p < 0.001$
	after 6 July	15	1.14	0.36	-56.9	+0.656	$p < 0.01$
	all dates	46	1.20	0.23	-36.36	+0.607	$p < 0.001$
Pout, Haddock and Whiting	before 7 July	31	-0.55	0.16	60.0	-0.547	$p < 0.01$
	after 6 July	15	-0.87	0.31	123.8	-0.613	$p < 0.02$
	all dates	46	-0.94	0.19	109.66	-0.592	$p < 0.001$
Barnacle Mussel	before 7 July	31	-0.07	0.02	6.7	-0.545	$p < 0.02$
	after 6 July	15	-0.26	0.14	27.2	-0.476	not significant
	all dates	46	-0.20	0.05	3.7	-0.492	$p < 0.001$
Bird, Mammal Egg	before 7 July	31	-0.03	0.02	4.4	-0.257	not significant
	after 6 July	15	-0.01	0.07	5.8	-0.021	not significant
	all dates	46	-0.06	0.03	7.4	-0.264	not significant

feed on sandeels, the fish obtained from fishing boat waste may represent more than half the diet in some years in terms of numbers of feeds taken by breeders. From this point of view it is worth noting that both 1975 and 1976 were apparently better years than average in terms of breeding success, with very few Great Skua chicks starving; while this could have been due to consistent high levels of fishing activity around Foula in these two years, it is unlikely that sandeel availability would have been greater in the years of poorer breeding success. Thus, not only does fishing waste form a very important part of the Great Skua diet, but it may also be critically important in providing an alternative food supply at times when sandeels are not available, thus saving chicks from starvation and susceptibility to predation. In relation to the amount of food that they require, nonbreeders spend considerably more time foraging than do breeders (which need to feed a mate and chicks as well as themselves), so nonbreeders may either be less efficient at foraging, or may have less reason to maximise their attendance at the colony by minimising foraging time. The result of this difference is that nonbreeders take a higher proportion of barnacles and mussels than breeders, because by spending longer at sea they are more likely to chance upon these, and also take a higher proportion of fish from fishing boats and fewer sandeels than breeders. Nonbreeders may be excluded from feeding on sandeels by breeders. This possibility is supported by the tendency for the difference in the percentage of sandeel in the diets of chicks and nonbreeders to be highest when sandeels are least abundant (figure 17), although a similar relationship does not seem to exist between breeders and nonbreeders. Competition for space above surface sandeel shoals certainly occurs. Although I was unable to quantify this, there were regular patterns in the distribution of the

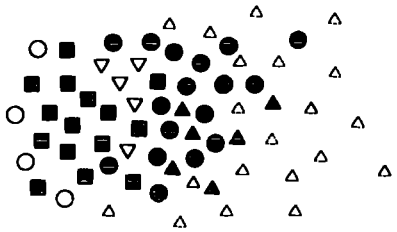
different seabird species feeding on shoals of sandeels (figure 23) which indicated that some individuals were being excluded from the best feeding positions by the dominance of other individuals or species. This may not be the only reason for the difference in diet, as foraging behind fishing boats is more time consuming than fishing for sandeels, so breeders may be under greater pressure to minimise foraging time than nonbreeders. Although requiring a lot of loafing time waiting for boats to begin sorting of the catch, following fishing boats may provide the least strenuous feeding technique, which may be a more important criterion to nonbreeders. The extent to which breeders or nonbreeders feed on offal from gutted fish is something that I have been unable to estimate. Offal leaves no trace in regurgitated pellets. It certainly is taken by Great Skuas following fishing boats, probably mainly by nonbreeders, and as the volume of offal produced by fishing is similar to the volume of rejected fish, it may be an important food source also.

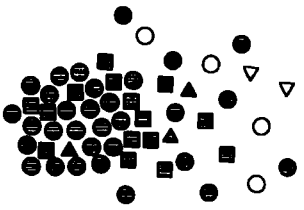
Skuas are well known for their habit of stealing fish from other seabirds (kleptoparasitism). As almost all the seabirds breeding on Foula feed almost exclusively on sandeels, it is reasonable to assume that almost all the fish stolen by skuas are sandeels. It is difficult to estimate what proportion of the sandeels eaten by Great Skuas are obtained by kleptoparasitism and what proportion by fishing on sandeel shoals. As the numbers of each seabird species vary only a little from year to year and all Auks and Kittiwakes feed almost exclusively on sandeels, it seems unlikely that the availability of seabirds for Great Skuas to rob would vary much from year to year, making it difficult to explain the differences in diet between years if most sandeels were obtained by kleptoparasitism. The striking fluctuations in the proportion of sandeels in the diet from week to week through a single

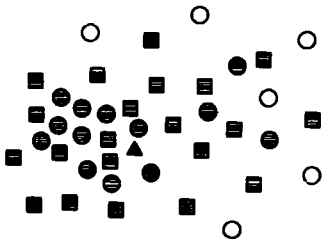
Figure 23. Diagrammatic representations of four typical feeding flocks of seabirds over shoals of sandeels, observed from Foula in summer 1975 and summer 1976. In each case the flock is following the shoal of fish which is running from right to left. Each symbol represents five birds:

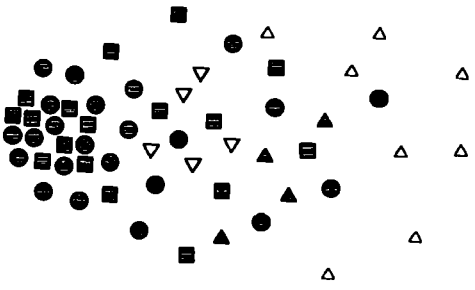
- ● Great Skuas
- ■ Fulmars
- ▲ Great Black-backed Gulls
- ○ Shags
- ▽ Gannets
- △ Auks, chiefly Guillemots

Great Skuas and Fulmars tend to dominate at the head of the fish shoal and diving species tend to occur at the tail and edges of the shoal.









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season (see below) are also difficult to explain if most sandeels were taken by kleptoparasitism as numbers of seabird carrying sandeels will vary only slowly and smoothly through the season. For these reasons it seems more likely that sandeels are obtained mainly by fishing on shoals, the presence of which vary both spatially and temporally in an apparently unpredictable fashion.

The behavioural aspects of kleptoparasitism by Great and Arctic Skuas are analysed in detail in section 6. It is sufficient here to point out reasons why this cannot be an important feeding method for Great Skuas. On Foula, Great Skuas outnumber Arctic Skuas by more than 10 to 1. It is more common to see Arctic Skuas robbing seabirds around most parts of the island's coastline, although Great Skuas, being larger birds, have twice the energy requirement of the smaller species. It is accepted that Arctic Skuas do obtain almost all their food by kleptoparasitism at British, Faroese and Icelandic breeding colonies (Salomonsen 1935, Cramp et al. 1974). Thus, if the daily food intake obtained through kleptoparasitism by the Great Skua population of Foula is roughly equal to the total intake of the Foula Arctic Skua population, it would represent only 5% of the total energy demand of the population. Little weight should be put on this statistic, as the calculation is a very crude one, but it does suggest the same as was concluded earlier; that kleptoparasitism is only a minor feeding technique of Great Skuas. At both observation sites where chases by skuas were recorded (see section 6), the rate of chases per hour by Great Skuas varied much more between observations than the rate of chases by Arctic Skuas (table 66). This difference appears to be due in part to weather conditions and in part of fish availability. Arctic Skuas chase seabirds as their principal feeding method, so are little affected by weather because they need their daily food ration;

Table 66. Mean, Standard Deviation and coefficient of variation of rates of kleptoparasitic chases by Great Skuas and Arctic Skuas at two sites off Foula where these were studied quantitatively in 1975 and 1976.

Site	Species	Kleptoparasitic chases per hour; mean	standard deviation	coefficient of variation
East Hoevdi	Great Skua	18.50	12.85	69.46
	Arctic Skua	5.12	2.48	48.44
North Hoevdi	Great Skua	1.96	1.05	53.57
	Arctic Skua	15.82	6.16	38.94

Great Skuas only resort to kleptoparasitism either when sandeel shoals are scarce, or when misty weather makes kleptoparasitism a more rewarding activity (see section 6).

Seasonal and annual differences in diet

It is difficult to obtain sufficient samples of regurgitates from chicks to compare seasonal trends in diet composition, as only 3.8% of chicks regurgitate on handling; no attempts were made to encourage chicks to regurgitate, either physically or by use of emetics. I showed earlier that chicks are fed mainly on sandeels even when sandeels are difficult to obtain, so chick diet would be a poor reflection of seasonal changes in food availability. Chicks do not regurgitate pellets, so pellets found in territories are from adults. When eggs hatch, adults spend progressively less time on their territorial mounds and tend to move around the territory with the chicks. This makes locating pellets difficult, and it becomes impossible to be certain that the pellets found are fresh. Thus comparisons of diets are most easily made using pellets collected from marked and regularly cleared areas on nonbreeder club sites. The diets of breeders and nonbreeders differ only slightly, and the difference appears to be consistent; breeders take 15% more sandeels than non-breeders, slightly fewer "other items", slightly more birds, mammals and eggs, and fewer reject fish from fishing boats (table 52). Thus nonbreeder pellet frequencies are taken to be the best indication of seasonal trends in food availability in the two years as nonbreeders are less constrained in diet than breeders. Changes in corrected pellet type frequencies taken by nonbreeders through the 1975 and 1976 seasons are shown in figures 24 and 25. The correlation between the

Figure 24. The diet of nonbreeding Great Skuas through 1975, determined by pellet analysis: percentages of feeds of sandeels, fishing boat rejects (Norway Pout, Haddock, Whiting, Blue Whiting, Redfish or Plaice) or other items (mainly Barnacle, Mussel, Rabbit or egg), against date.

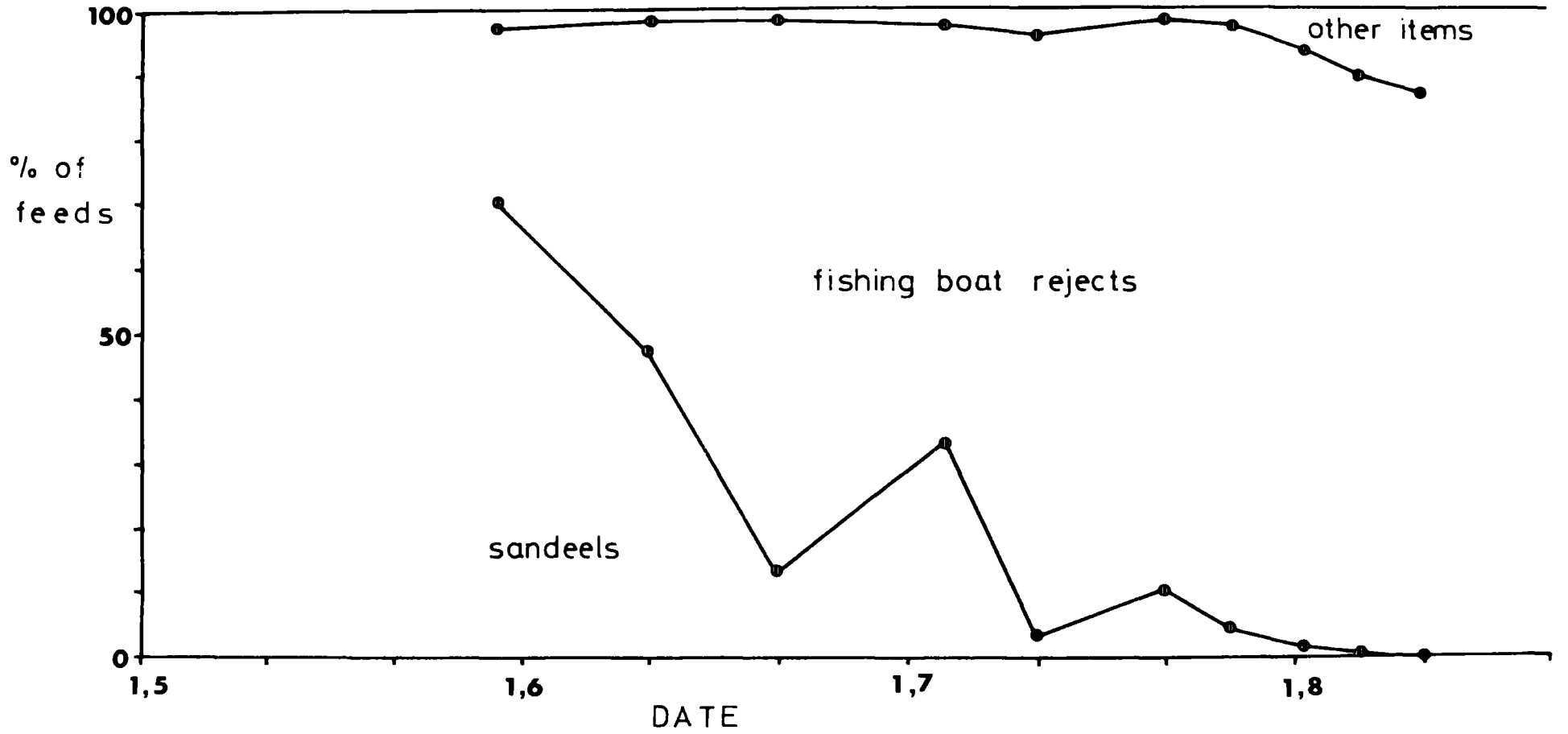
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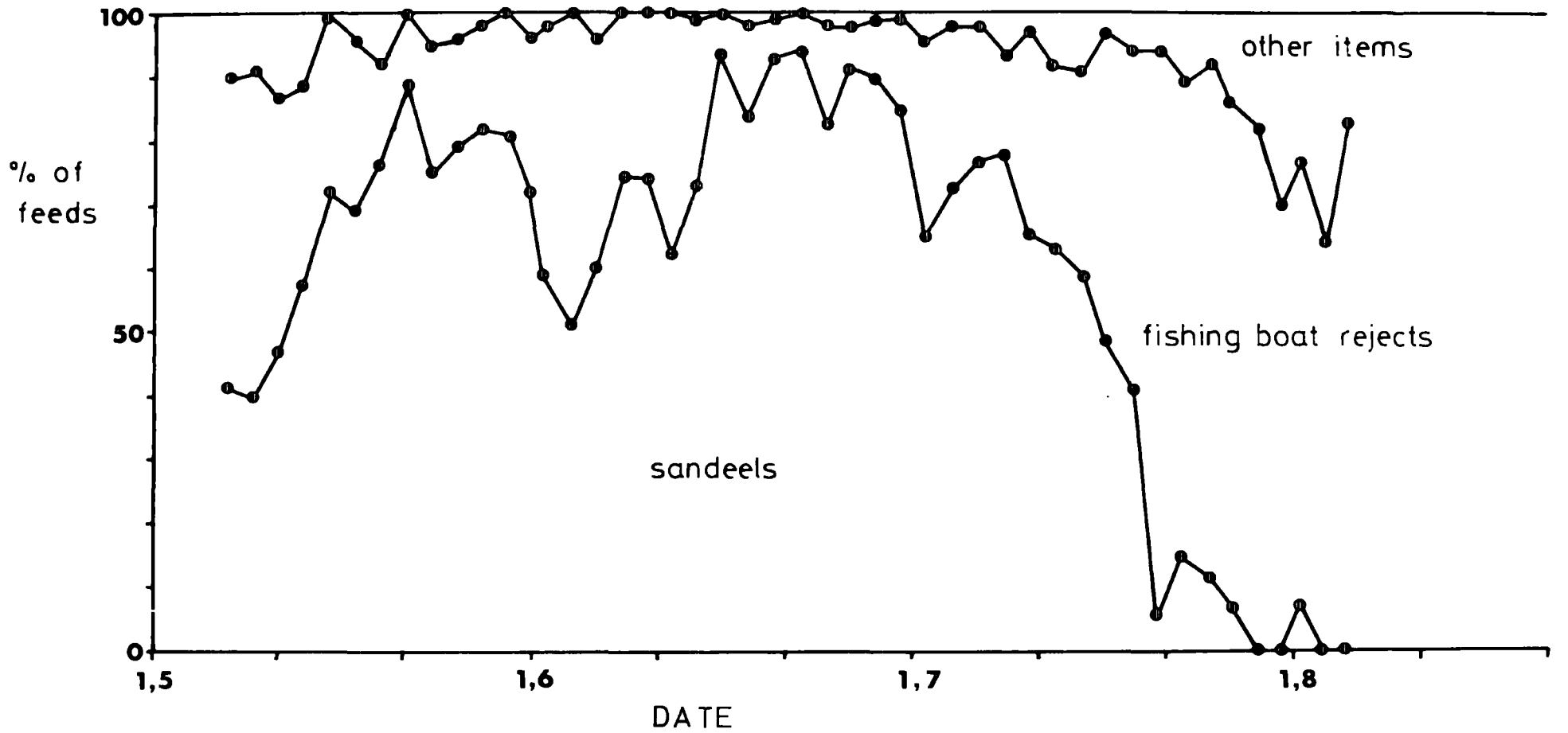
Figure 25. The diet of nonbreeding Great Skuas through 1976, determined by pellet analysis.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frequency of sandeel pellets in the diet of nonbreeders in 1976 (figure 25) and the percentage attendance of breeders on their territory in 1976 (figure 21) can be seen visually. The pattern in 1975 is rather different. There is a similar decline in the frequency of sandeels in the diet between May and August, but in 1975 this decline began during May, and Norway Pout/Haddock/Whiting predominated in the diet after mid-June. In 1976 sandeels remained dominant until mid-July, then crashed to zero. In 1975 the mean percentage of breeders in their territories was slightly lower than the 1976 value on most dates, but averages only 5% less, suggesting that the predominance of Norway Pout/Haddock/Whiting in the diet may have been partly due to greater availability of these in 1975, rather than shortage of sandeels, so that the foraging time of birds feeding from boats was only slightly greater than that of birds feeding on sandeels. The seasonal improvement in sandeel availability in May, switch from sandeels to Norway Pout/Haddock/Whiting in June or July, and the decline in Norway Pout/Haddock/Whiting availability in late July or August would appear to be the normal seasonal pattern, as it was observed qualitatively in the other years I visited Foula. The pattern is consistent with the known behaviour of sandeels, which are most frequently found as surface shoals in May and June (Pearson 1964).

It is of interest to compare the species of fish taken by breeding and nonbreeding Great Skuas and nonbreeding Great Black-backed Gulls at fishing boats, as the Great Black-backed Gull is the seabird with the most similar feeding ecology to the Great Skua. Great Black-backed Gull pellets were also collected regularly in 1975 and 1976 from a loafing area used by about 200 nonbreeding birds, mostly in immature plumages. Sandeel otoliths are not retained to be regurgitated, but are voided in the faeces by Great Black-backed Gulls. This makes it

difficult to determine the amounts of each item in the diet, but sandeel otoliths were never found in more than 30% of scats examined on any occasion, suggesting that larger fish form the bulk of the diet of these birds.

The fish taken at boats may be divided into four groups; Norway Pout, Haddock, Whiting, other fish species (i.e. Redfish, Blue Whiting, Plaice) of which the last category is far less numerous than any other. Comparing first the numbers of otoliths of fish taken by breeding and nonbreeding Great Skuas through 1976 (table 67) shows that any difference in species taken is very small, the only clear trend being the tendency of nonbreeders to take small numbers of "other species" which breeders seem to avoid ($X^2 = 8.73$, df = 3, $p < 0.05$). The numbers of each species taken by nonbreeders attached to particular clubs show no difference between clubs when collections through the whole of the 1976 season are compared (table 68, $X^2_3 = 6.42$, ns), but show a signigicant difference when the season is divided into ten day periods (table 69, $X^2_{12} = 30.30$, $p < 0.005$). This suggests that birds from the same club may tend to feed at the same fishing boat, which may be fishing for one species in particular, but that these heterogeneities are not consistent preferences of the birds of a particular club as they are evened out through time.

There are pronounced and consistent differences in fish taken by Great Skuas and Great Black-backed Gulls (tables 70 and 71). The five values of X^2_3, (37.3, 12.1, 27.3, 24.8, 99.6) are all statistically significant ($p < 0.001$ in every case), and all show Great Skua nonbreeders to take more Norway Pout than Great Black-backed Gull nonbreeders do, and fewer "other species".

The proportions of each fish species taken also vary between sampling dates, both for Great Skua nonbreeders in 1975 (table 72,

Table 67. A comparison fo fish taken by breeding and nonbreeding Great Skuas on Foula between 1 May and 10 June 1976, as shown by otolith counts. (Expected numbers if no difference with status are in parentheses).

Fish species	Taken by breeders	Taken by nonbreeders	Total
Norway Pout	26 (26.0)	64 (64.0)	90
Haddock	119 (107.3)	252 (263.7)	371
Whiting	76 (83.3)	212 (204.7)	288
"other species"	0 (4.3)	15 (10.7)	15

Table 68. A comparison of fish taken on different dates at two club sites; collections through the whole of 1976 season are compared between Bottle and Strem Ness club sites. (Expected values in parentheses)

Fish species	Otoliths from Bottle club site	Otoliths from Strem Ness club site	Total
Norway Pout	29 (23.8)	35 (40.2)	64
Haddock	102 (93.8)	150 (158.2)	252
Whiting	66 (78.9)	146 (133.1)	212
"other species"	5 (5.6)	10 (9.4)	15

Table 69. A comparison of fish taken at two Great Skua nonbreeder club sites over four ten-day intervals in 1976. (Expected values in parentheses)

Fish species	Otoliths from Bottle club				Otoliths from Strem Ness club			
	May 1 - 10	May 11 - 20	May 21 - 31	June 1 - 10	May 1 - 10	May 11 - 20	May 21 - 31	June 1 - 10
Norway Pout	9 (12.8)	14 (5.8)	5 (4.1)	1 (2.3)	18 (14.2)	5 (13.2)	7 (7.9)	5 (3.7)
Haddock	44 (40.0)	22 (21.9)	24 (22.3)	12 (12.0)	40 (44.0)	50 (50.1)	41 (42.7)	19 (19.0)
Whiting	14 (14.3)	18 (27.1)	16 (18.5)	18 (15.1)	16 (15.7)	71 (61.9)	38 (35.5)	21 (23.9)
"other species"	2 (1.9)	2 (1.2)	1 (1.0)	0 (1.5)	2 (2.1)	2 (2.8)	2 (2.0)	4 (2.5)

Table 70. Numbers of otoliths of each fish species taken by Great Skua nonbreeders and Great Black-backed Gull nonbreeders through 1975 and collected from club sites and loafing areas. (Expected values in parentheses).

Date	Species	Fish taken				
		Norway Pout	Haddock	Whiting	"others"	Total
24 June	Great Skua	41 (25.2)	97 (102.7)	59 (64.6)	1 (5.5)	198
	Great B.-b. Gull	0 (15.8)	70 (64.3)	46 (40.4)	8 (3.5)	124
10 July	Great Skua	27 (19.8)	50 (54.2)	59 (61.5)	1 (1.5)	137
	Great B.-b. Gull	0 (7.2)	24 (19.8)	25 (22.5)	1 (0.5)	50
25 July	Great Skua	34 (22.2)	33 (41.8)	59 (60.7)	0 (1.3)	126
	Great B.-b. Gull	0 (11.8)	31 (22.2)	34 (32.3)	2 (0.7)	67

Table 71. Numbers of otoliths of each fish species taken by Great Skuas and Great Black-backed Gulls and collected from nonbreeding clubs and loafing sites in 1976. (Expected values in parentheses).

Dates	Species	Fish taken				
		Norway Pout	Haddock	Whiting	"others"	Total
1 May to 10 June	Great Skua	90 (76.5)	371 (380.7)	288 (287.2)	15 (19.6)	764
	Great B.-b. Gull	0 (13.5)	77 (67.3)	50 (50.8)	8 (3.4)	135
11 June to 30 July	Great Skua	54 (21.8)	71 (99.1)	133 (125.1)	4 (15.9)	262
	Great B.-b. Gull	9 (41.2)	215 (186.9)	228 (235.9)	42 (30.1)	494

X^2 = 71.0, df = 24, $p < 0.005$) and 1976 (table 73, X^2 = 120.9, df = 16, $p < 0.005$), and for Great Black-backed Gull nonbreeders in 1976 (Table 74, X^2 = 31.9, df = 16, $p < 0.025$), but not in 1975 (table 75, X^2 = 5.5, df = 4, ns). Clearly these heterogeneities reflect differences in the fish catches and composition of catches taken by fishermen, but this may be due to selection by fishing boats, to changes in fish availability or to chance catches of shoals of particular species on different dates.

There is a tendency for the fish taken by Great Black-backed Gulls to vary through the season. Too few time periods were examined in 1975 to show this, but in 1976 there were significant correlations between date and proportions of Haddock and Whiting in the diet. Similar correlations were found in the nonbreeding Great Skua diet through the same season, indicating that Haddock availability relative to Whiting availability decreases through the summer. The correlations are not statistically significant for Great Skua samples, probably partly because of the confounding effects of Norway Pout availability, but mainly because the sample size is small (only nine time intervals), as the correlation coefficients themselves are high (table 76).

Table 76. Correlations between percentages of each fish type taken at fishing boats and date through the breeding season in 1976.

Species	Prey	Correlation with date	significance t	p	slope
Great B.-b. Gull	Haddock	- 0.838	4.07	0.01	- 3.72
	Whiting	+ 0.703	2.62	0.05	+ 2.63
Great Skua	Haddock	- 0.662	2.33	ns	- 3.57
	Whiting	+ 0.518	1.60	ns	+ 2.83
	Norway Pout	+ 0.286	0.79	ns	+ 0.83

Table 72. Numbers of otoliths of each fish species in collected pellets from Great Skua club areas on different dates in 1975, (excluding sandeel), expected values if no heterogeneity existed are given in parentheses.

Date of collection	Fish taken				
	Norway Pout	Haddock	Whiting	"others"	Total
28 May	30 (26.5)	44 (39.3)	29 (37.4)	1 (0.8)	104
24 June	41 (50.5)	97 (74.8)	59 (71.3)	1 (1.5)	198
4 July	27 (33.4)	55 (49.5)	45 (47.2)	4 (1.0)	131
10 July	27 (35.0)	50 (51.7)	59 (49.3)	1 (1.0)	137
20 July	30 (15.8)	16 (23.4)	16 (22.3)	0 (0.5)	62
25 July	34 (32.1)	33 (47.6)	59 (45.4)	0 (0.9)	126
1 August	46 (39.3)	57 (58.1)	50 (55.4)	1 (1.1)	154
5 August	5 (12.0)	23 (17.7)	19 (16.9)	0 (0.4)	47
10 August	35 (30.4)	32 (44.9)	52 (42.8)	0 (0.9)	119
Totals:	275	407	388	8	1078

Table 73. Numbers of otoliths of each fish species in collected pellets from Great Skua club areas on different dates in 1976, (excluding sandeel). Expected values if no heterogeneity existed are given in parentheses.

Date of Collection	Fish taken						
	Norway Pout and "others"		Haddock		Whiting		Total
10 May	47	(37.5)	146	(101.7)	43	(96.8)	236
20 May	32	(38.6)	96	(104.7)	115	(99.7)	243
31 May	16	(24.1)	75	(65.5)	61	(62.4)	152
10 June	10	(21.1)	54	(57.3)	69	(54.6)	133
20 June	21	(9.4)	15	(25.4)	23	(24.2)	59
30 June	6	(6.8)	6	(18.5)	31	(17.6)	43
10 July	8	(8.4)	18	(22.8)	27	(21.8)	53
20 July	9	(7.0)	9	(19.0)	26	(18.1)	44
30 July	14	(10.0)	23	(27.1)	26	(25.9)	63
Totals:	163		442		421		1026

Table 74. Numbers of otoliths of each fish species in collected pellets from Great Black-backed Gull loafing areas on different dates in 1976, expected values if no heterogeneity existed are given in parentheses.

Date of collection	Fish taken						
	Haddock		Whiting		"others"		Total
10 May	22	(13.5)	7	(12.8)	0	(2.7)	29
20 May	10	(9.3)	10	(8.8)	0	(1.9)	20
31 May	31	(27.4)	22	(26.1)	6	(5.5)	59
10 June	14	(12.5)	11	(11.9)	2	(2.5)	27
20 June	88	(79.4)	65	(75.6)	18	(16.0)	171
30 June	31	(30.6)	25	(29.2)	10	(6.2)	66
10 July	25	(28.3)	31	(27.0)	5	(5.7)	61
20 July	32	(46.4)	57	(44.2)	11	(9.4)	100
30 July	39	(44.6)	50	(42.4)	7	(9.0)	96
Totals:	292		278		59		629

Table 75. Numbers of otoliths of each fish species in collected pellets from Great Black-backed Gull loafing areas on different dates in 1975, expected values if no heterogeneity existed are given in parentheses.

Date of collection	Fish taken				"others"		Total
	Haddock		Whiting				
23 June	70	(64.3)	46	(54.0)	8	(5.7)	124
10 July	24	(25.9)	25	(21.8)	1	(2.3)	50
25 July	31	(34.8)	34	(29.2)	2	(3.3)	67
Totals:	125		105		11		241

The proportion of Haddock in the diets of the two species also shows a significant positive correlation ($r = +0.740$, $df = 7$, $t = 2.91$, $p < 0.05$) and the proportions of Whiting are also positively correlated ($r = +0.524$, $df = 7$, $t = 1.63$, ns). These correlations indicate that the Great Skuas and Great Black-backed Gulls are obtaining their food from very similar or the same sources (i.e. fishing boats) and suggest that the differences shown in the diets of the two species could be due to competition. The presence of "other fish species" in the Great Black-backed Gull diet but scarcity in Great Skua diet may simply reflect the ability of Great Black-backed Gulls to swallow larger fish, as these prey items (particularly Redfish and Blue Whiting) are larger than the Haddock and Whiting taken by both birds, and may be too large for Great Skuas to handle efficiently. This would agree with the observation that adults take fewer "other species" than nonbreeders, as breeders would be expected to be more efficient and selective feeders. Norway Pout may be ignored by Great Black-backed Gulls as they are smaller than Haddock and Whiting, but the scarcity of this fish in the diet of Great Black-backed Gulls is surprisingly pronounced.

Comparing the numbers of each species of fish represented in the annual totals of otoliths from Great Skua pellets from nonbreeders (tables 70 and 71), shows a significant difference in the two seasons (table 77, $X^2_3 = 46.89$, $p < 0.005$). In 1976 the diet contained a smaller proportion of Norway Pout, and contained a few more "other species" although these remained below 2% of the fish taken at boats and the deficiency of Norway Pout was balanced by a higher proportion of both Haddock and Whiting.

Presumably these differences result from variations in year class strength between cohorts of these species, or from differences in the intended catches of fishing boats in the area around Foula in these

Table 77. A comparison of the total number of otoliths of each fish species taken at fishing boats by nonbreeding Great Skuas through the 1975 and 1976 seasons on Foula; expected values if there was no difference between seasons are given in parentheses.

Year	Fish Taken				
	Norway Pout	Haddock	Whiting	"others"	Total
1975	275 (214.7)	407 (435.0)	388 (414.5)	8 (13.8)	1078
1976	144 (204.3)	442 (414.0)	421 (394.5)	19 (13.2)	1026
Totals	419	849	809	27	2104

two summers.

Although the level of predation on birds, mammals and eggs could not be shown to be related to preferred food availability on a day to day basis in 1976, it is clear that predation on birds varies in intensity between years, and also in the relative numbers of each species killed. It would appear that food availability over longer periods than one or two day intervals determines the scale of predation on birds. This is a reasonable conclusion if the bulk of predation on birds is by females on territories taking advantage of infrequently occurring opportunities.

Each year from 1969 to 1976, Brathay expedition members have collected corpses of birds on Foula, and recorded which of these appear to have been killed by Great Skuas. In 1975, corpses were recorded independently by myself and by Brathay. Of 125 found by myself, 103 were also found by Brathay. This suggests a search efficiency, of 82%, but this is likely to be an overestimate as both recorders are likely to have overlooked the same inconspicuous corpses. Thus a value of 75% finding success will be assumed. The annually repetitive nature of Brathay expeditions means that corpse finding efficiency should remain constant. The total number of bird kills on Foula by Great Skuas, corrected to allow for searching efficiency of 75% (table 78) indicates a fourfold difference in intensity between years, a considerable consistent difference in predation intensity on different species, and large variations in the proportions of the main prey species killed in different years.

Differences in predation intensity on different species presumably reflect differences in the ease with which each species can be killed, slightly modified by individual or colony-traditional preferences. Differences in the intensity of predation on birds between years suggest

Table 78. Number of kills of each bird species by Great Skuas on Foula, assuming a corpse finding efficiency of 75%.

Species	Age	1969	1970	1971	1972	1973	1974	1975	1976
Great Skua	chick	10	15	33	70	60	22	40	13
	juvenile	25	50	200	217	151	145	73	44
Puffin	adult	60	23	59	157	194	115	71	54
	juvenile	5	2	9	0	0	12	1	5
Kittiwake	adult	2	1	5	3	5	0	13	4
	juvenile	149	14	163	73	161	332	105	63
Arctic Skua	adult	20	3	11	19	3	21	17	7
	juvenile	51	14	72	56	43	35	26	36
Red-throated Diver	chick	0	0	0	4	0	1	0	1
Fulmar	adult	2	2	3	0	6	1	20	0
Storm Petrel	adult	4	0	0	0	5	9	1	1
Shag	adult	0	21	14	1	1	0	11	0
Eider	adult	0	5	9	8	9	0	7	7
Oystercatcher	adult	0	3	5	4	12	8	0	1
Lesser Black-backed Gull	adult	1	4	2	3	12	0	0	0
Herring Gull	adult	1	3	8	11	17	6	4	1
Great Black-backed Gull	adult	1	1	7	13	2	3	4	0
Common Gull	adult	0	1	0	13	0	0	2	0
Arctic Tern	adult	7	12	0	6	1	1	4	1
Black Guillemot	adult	8	4	2	19	13	7	7	3
All other species		6	0	10	16	16	0	14	6
Total kills in the season		352	178	612	693	711	718	420	247

that both 1975 and 1976 were of above average food availability, as few birds were killed.

As systematic pellet collections were not made in earlier years, this conclusion cannot be directly confirmed, but casual observation did suggest that some chicks died of starvation in 1973 and 1974, while this was almost unknown in 1975 and 1976. Furthermore, in the four years with high bird predation (1971 - 74) there was a higher proportion of Great Skuas chicks killed than in the four years of low predation (1969, 70, 75 and 76) (table 79) ($X^2 = 31.4$, df = 1, $p < 0.001$).

Table 79. Numbers of Great Skuas and other birds (before correction to allow for corpse finding efficiency) killed by Great Skuas on Foula in years of high and low predation on birds. Expected values, assuming no heterogeneity, are given in parentheses.

	Number of kills found		
	Great Skuas	All other species	Total
In years of high predation on birds (1971, 72, 73, 74)	674 (610)	1377 (1441)	2051
In years of low predation on birds (1969, 70, 75, 76)	203 (267)	695 (631)	898

Killing of Great Skua chicks and fledglings is much more likely to occur under conditions of food shortage because under good food conditions it is prevented by the protection of the parents. This indicates that years of food scarcity result in greater predation on

birds, and with increasing food scarcity, there is a proportionately greater tendency for Great Skua chicks to be taken. Differences in the proportions of other main prey species taken in each year may result from differences in the time of food shortage during the season. Kittiwake juveniles are only available over a short period immediately after the fledging of this species, which occurs between mid-July and early August. Arctic Skua juveniles are available only between fledging and dispersal, and presumably become more difficult to kill as their flying ability matures. They will only be a ready food source during the middle of July. Adult Puffins are probably most easily caught when busy with chick rearing, which lasts from early June to early August. "Others" killed are mainly adults of a variety of species present through the Great Skua breeding season, so are probably continuously available. The main differences between the bird species taken in 1975 and 1976 are that a larger proportion of "other species" was taken in 1975. This suggests that food shortage was more serious earlier in the season in 1975, and the larger total number of birds killed in 1975 suggests that food was generally poorer than in 1976. Both of these conclusions are supported by the results of measurements of time spent on territory (figure 21) and sandeel availability in the two seasons (figures 24 and 25).

Impact of predation on birds and mammals

Great Skuas feed on carrion as well as killing birds and mammals, and it is impossible to decide from corpse or pellet evidence whether the item was killed or not. Large numbers of seabird chicks and fledglings die in July and August, but some of these are not eaten, while Great Skuas can be seen attacking and killing apparently

healthy individuals. It seems likely that at least half of the feeds on birds and mammals are of carrion; with over 200,000 adult seabirds at Foula each summer and a probable mortality of 1 or 2% of these during this period, then 2000 to 4000 corpses might be expected on which Great Skuas could feed, with another 3000 to 6000 corpses of chicks available in July to August. There are only two or three pairs of Hooded Crows and four or five pairs of Ravens on Foula; Fulmars and Great Black-backed Gulls are the main competitors for carrion, and only the Fulmar on the sea is able to dispossess Great Skuas of corpses. As Fulmars seem only to consume the offal, Great Skuas are soon allowed to return to the corpse to eat the meat.

Only a very small number of Rabbits are eaten on Foula by Great Skuas. The average number recorded as having been eaten by skuas over the years 1969 to 1976 was only 21, although there must be several thousand individuals in the population. Only two pellets of Rabbit remains were found of the 1535 collected pellets in 1976 (0.13 %). Even if these were all due to predation the Great Skua could not have any detectable influence on the numbers or age-structure of the Rabbit population. Predation of Hedgehogs has been recorded on three occasions, but is equally unimportant. Predation levels on mammals in other parts of the North Atlantic range of the Great Skua can also be regarded as irrelevant to the prey species.

On Foula, eggs of its own species form the majority of those consumed by Great Skuas. Elsewhere, due to lower nesting density (section 5), fewer skua eggs are stolen, but nowhere does egg stealing form a major part of the diet, except for a very small number of specialist individuals (e.g. Bayes et al.1964). The Red-throated Diver is the only other species on Foula which suffers a loss of more than 0.1% of its eggs each year to Great Skua predation. Breeding

success of this species on Foula has been recorded in every year since 1956, but causes of breeding failure have only been documented in detail in 1975 and 1976 (table 80). Great Skuas accounted for 79% of all Red-throated Diver eggs lost in 1975, and 50% of losses in 1976, but because a large proportion of lost clutches were replaced, chick production per pair on Foula was as high as recorded in any other part of Shetland (Bundy 1976, Scottish Bird Reports, Shetland Bird Reports). This is no doubt partly due to the low level of human disturbance on Foula. Greater human disturbance would give skuas more opportunities to steal eggs.

Predation by Great Skuas on birds has been suggested as a cause of declines in Arctic Skua (Pennie 1948), Kittiwake (Venables & Venables 1955), Arctic Tern (Meinertzhagen 1941), Herring Gull, Lesser Black-backed Gull, Common Gull, Black-headed Gull, Arctic Tern, Red-throated Diver and Whimbrel (Stenhouse 1926) populations in various parts of Shetland. None of these authors presented quantitative data in support of their assertions, but their views have received general acceptance.

The total energy requirement of the Foula Great Skua population in one season is 33×10^7 kcals (table 44), which consists of fish and "other items" (99%) and birds and mammals (1%) (table 53). Using the values in table 81 the total number of birds eaten each season can be estimated to be 10,000.

The total number of corpses attributed to Great Skua predation on Foula varied only between 178 and 718 in the years 1969 to 1976 (table 78), with only 420 and 247 corpses in the years of pellet study. Presumably most birds were eaten at sea so the corpses could not be recorded. Corpse records show only what bird prey is eaten on Foula, while pellets include birds killed and eaten at sea.

Table 80. Breeding success of Red-throated Divers on Foula in 1975 and 1976.

Category	1975	1976
Breeding pairs	11	11
Clutches lost to predators	7	4
Clutches replaced	4	3
Eggs laid	29	27
Eggs taken by Great Skuas	15	7
Eggs taken by humans	0	4
Eggs deserted	4	3
Eggs hatched	10	13
Eggs hatched per breeding pair	0.91	1.18

Table 81. Parameters required to estimate the number of birds eaten each season by the Foula Great Skua population.

Parameter	Value
Weight of average "feed" on fish	90 g
Calorific value of fish	1.1 kcals g^{-1}
Calorific value of average feed	100 kcals
Number of feeds from each bird corpse	3
Energy requirement of colony	3×10^8 kcals
Number of feeds on birds required	3×10^6
Number of birds eaten (some as carrion)	10,000

A comparison of species frequencies by the two methods, allowing for differences in bird species eaten by breeders and nonbreeders, shows that corpse records greatly underestimate the proportion of Kittiwakes and Storm Petrels, and greatly overestimate the proportion of skuas eaten (table 82).

Although Guillemots and Razorbills are numerous at Foula, and their skulls and legs are incorporated into Great Skua pellets as often as juvenile Puffin heads or adult Puffin legs, almost all auk corpses found on Foula are of Puffins. The Puffin is the only auk which regularly flies over the island, so that kills can be made over land. Presumably Guillemots and Razorbills are killed in numbers, but only on the sea. It seems reasonable to assume that virtually all the fledgling Great Skuas and fledgling and adult Arctic Skuas that are eaten are either killed or found dead on Foula, and therefore that the numbers of corpses of these species recorded in annual corpse collections are correct. Then from table 82 it can be crudely estimated that the 256 skua corpses found in 1975 and 1976 represent 2.9 % of the birds eaten in these two seasons. This estimate is no less crude than the earlier one of 10,000 birds eaten each season, but neither estimate is much greater than the potentially available total of bird corpses, so carrion could form a very large proportion of birds eaten. The species most likely to suffer from Great Skua predation are the Arctic Skua (discussed in section 6), the auks, which represent 50% of the avian diet, Storm Petrels, of which adults are eaten in numbers, and Kittiwakes, which represent 25% of the avian diet although many of these are taken as dead chicks from below colonies or as weak fledglings. Surveys of Foula seabird populations do not suggest that any of these species are presently declining in numbers.

Table 82. Numbers of birds eaten by Great Skuas on Foula in 1975 and 1976 compared to the proportions of different species represented in bird pellet material collected through the 1975 and 1976 seasons. The latter also contains remains of birds eaten at sea (see text). Values in parentheses are percentages of the total annual sample.

Food type	1975		1976		both years
	corpses	birds in pellets	corpses	birds in pellets	birds in pellets
Great Skua or Arctic Skua	156 (37.1)	8 (3.7)	100 (40.5)	0 (0.0)	8 (2.9)
Auks	83 (19.8)	121 (55.5)	64 (25.9)	32 (59.3)	153 (56.2)
Kittiwake	118 (28.1)	57 (26.2)	67 (27.1)	11 (20.4)	68 (25.0)
Shag	11 (2.6)	4 (1.8)	0 (0.0)	1 (1.9)	5 (1.8)
Storm Petrel	1 (0.2)	24 (11.0)	1 (0.4)	6 (11.1)	30 (11.0)
Other species	51 (12.1)	4 (1.8)	15 (6.1)	4 (7.5)	8 (2.9)
Totals	420	218	247	54	272

SECTION 5

BREEDING

Introduction

Studies of skua colonies in the Antarctic and sub-Antarctic (Downes et al. 1959, Eklund 1961, Young 1963, Reid 1967, Burton 1968, Wood 1970, 1971, Spellerberg 1971) have shown that, as has been found in other seabird species, young birds tend to breed later in the season and are less successful than experienced birds; breeding success is higher where nest density is low, possibly due largely to cannibalism (Burton 1970), and older chicks may kill their sibling under conditions of food scarcity.

To examine breeding on Foula, three areas were delimited, within which all Great Skua nests were marked. The area A was chosen to represent the highest nest density in the colony, B was of lower density, and C represented recently colonised parts of the colony. Areas B and C were studied in both 1975 and 1976. Area A was studied only in 1975. An advantage of the small area C was that all pairs there consisted of individually recognisable birds whose histories had been recorded since 1973, so their breeding could be examined in relation to previous breeding experience.

Perry (1948) gives details for the Great Skua colony on Noss in 1946 of the laying dates, hatching dates, incubation periods, intervals between the laying of each egg and between the hatching of each egg, and fledging periods and dates. This study gave similar data, which do not differ significantly from those obtained by Perry.

The eggs

At every study nest the following parameters were measured; egg colour (olive, brown, stone or blue), spot distribution (1. clumped at blunt pole; 2. clumped an blunt half of the egg; 3. uniformly distributed over egg), spot intensity (1-5; 1: very few spots. 5: heavily spotted), egg length and breadth, and from these were calculated shape index (100 x breadth / length) and internal volume (cm^3), (length(mm) x breadth(mm) x breadth(mm) x 0.00048), and egg weight, and from this an egg density index (egg weight / internal volume) was calculated. Where laying sequence was known, eggs were marked A and B with an indelible marker, where unknown they were marked a and b. Hatching sequence of eggs was recorded for as many study nests as possible. In 1976, 211 nests of known hatching sequence and 91 nests of known laying sequence were available for analysis. In 39 cases both laying and hatching sequences were known. In every case eggs hatched in the order in which they had been laid, although on a few occasions nests have been located with two chicks hatching simultaneously, so hatching order may very rarely be the reverse of the laying order.

All measured parameters showed differences between first and second laid eggs (table 83), but these differences are small compared to the variation between clutches.

Using a discriminant function, based on the differences between the two eggs in spot distribution, egg length, density index and ground colour (table 84), the eggs in 199 of 211 (94.3 %) clutches were correctly classified into the first and second laid categories. This function was then used to classify eggs in all nests where neither laying nor hatching sequence was known.

Drent (1970) showed that eggs lose approximately 15% of their

Table 83. Differences in measurements of first and second laid eggs of 211 two egg Great Skua clutches of known sequence studied in 1976 on Foula.

Parameter	Mean difference between 1st and 2nd eggs	S.D. of difference	S.E. of difference	t_{210}
Egg length	+ 2.34mm	2.32	0.16	14.6
Egg breadth	- 0.11mm	0.92	0.060	1.7
Egg volume	+ 2.41cm^3	3.42	0.24	10.0
Shape index	- 2.43	2.93	0.20	12.1
Egg density	- 0.012 g cm^{-3}	0.020	0.0013	9.2
Egg colour	+ 0.44	1.31	0.090	4.9
Intensity of spotting	+ 0.44	0.85	0.059	7.5
Spot distribution	+ 0.79	0.73	0.050	15.8

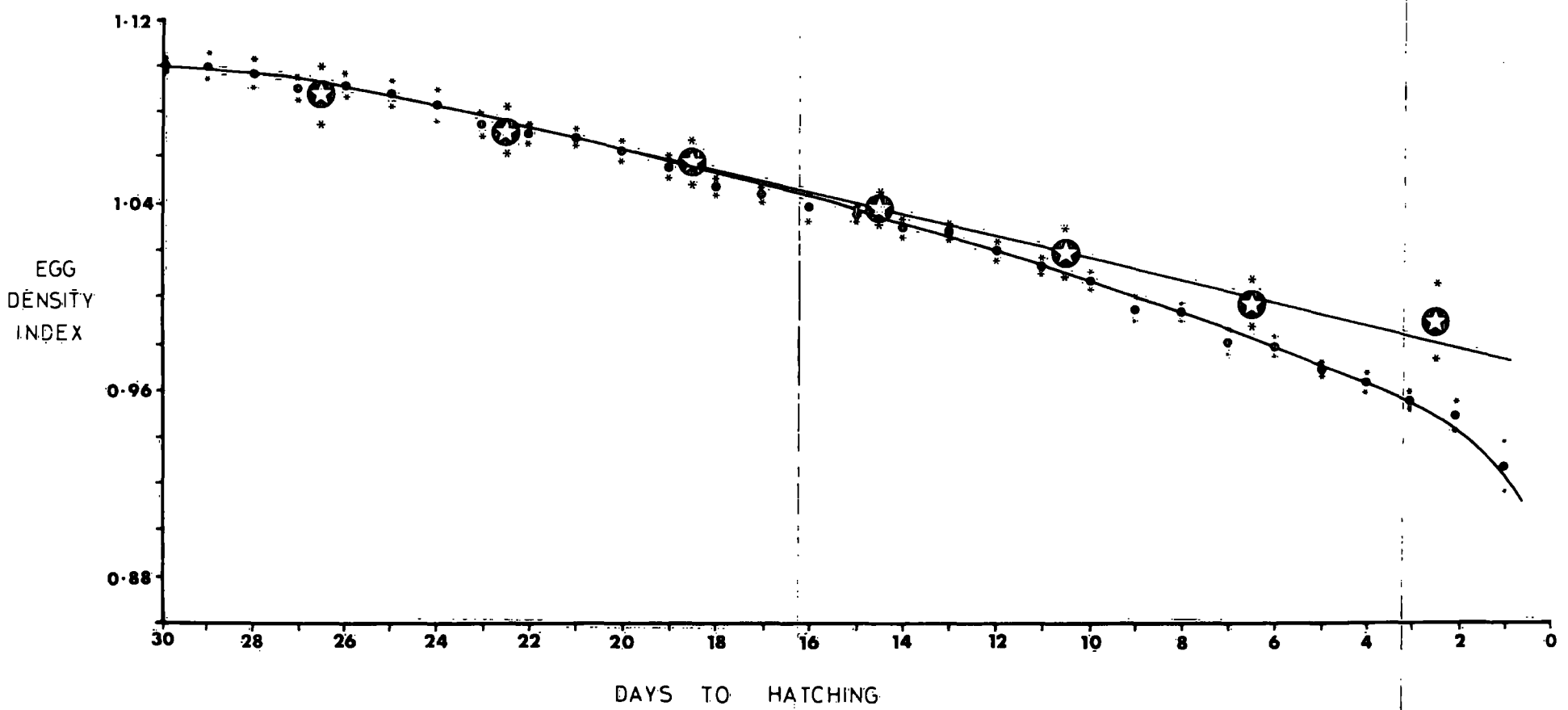
Table 84. Factors which discriminate between first and second laid eggs in Great Skua clutches of two eggs laid on Foula.

Parameter	Rao's V	Change in Rao's V	significance of change in Rao's V	discriminant function coefficient.
Difference in:				
spot distribution	492.4	492.4	$p < 0.001$	- 0.4944
egg lengths	850.4	358.0	$p < 0.001$	- 0.1301
egg densities	951.9	101.5	$p < 0.001$	37.9316
egg colours	1018.1	66.2	$p < 0.001$	- 0.1056

initial weight due to water loss during incubation. This loss is presumably the cause of the density difference between eggs in a clutch, as the first laid egg will have been incubated for 48 - 72 hours longer than the second. It also allows the hatching date of a clutch to be predicted. There is an almost linear reduction in density index up to the start of breathing by the embryo, which occurs two or three days before hatching (figure 26), by which stage it can be heard calling within the egg, and cracks are usually visible on the shell surface. Addled eggs follow the same curve, but without the increased water loss caused by chick hatching, the difference in density between addled and living eggs not being statistically significant until less than eight days before hatching (figure 26). Thus egg density index can be used to estimate the hatching date. This is particularly useful for clutches which fail to hatch and are of unknown laying date. It should be noted that the use of the constant 0.00048 (Coulson et al. 1969) in the determination of egg volume gives the internal egg volume, so the density index is not equal to density determined by flotation (which includes shell volume). Barth (1967) suggests a factor of 0.0005084 to give absolute densities (specific gravities) of eggs of Larids.

Egg parameters may vary consistently with parent age and with laying date, and it has been suggested that egg measurements could be used to examine the age structure of seabird colonies (Coulson 1963). In particular, egg volumes of Kittiwakes and Shags appear to decrease consistently in relation to laying date and are also smaller in younger birds for any given laying date (Coulson et al. 1969). An ability to determine the number of pairs recruiting into a breeding colony in a season by a single visit to that colony would be useful, both in studies of colony growth and in the practical monitoring of

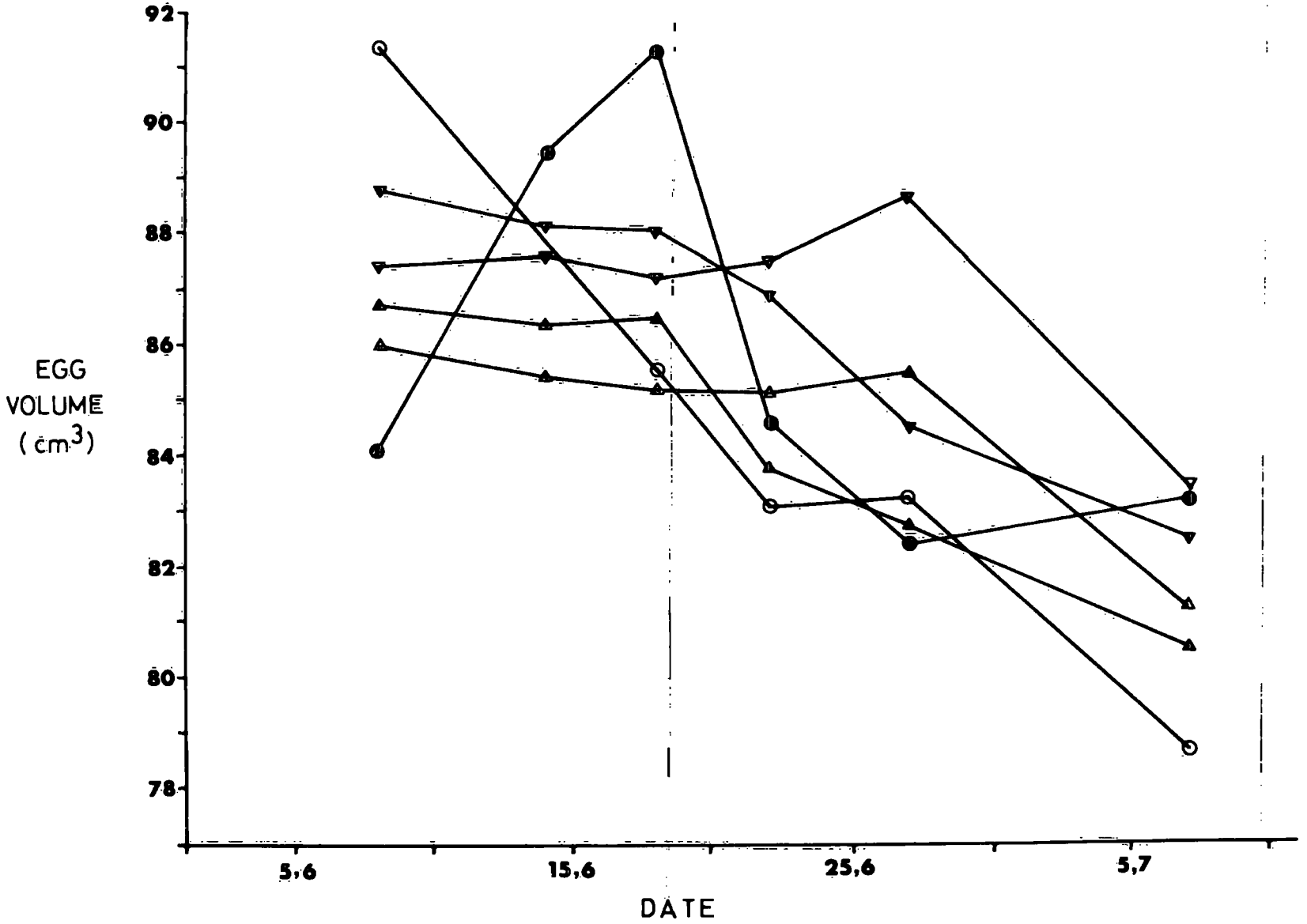
Figure 26. Density indices of fertile and addled eggs in relation to the number of days to hatching. Addled egg mean densities are marked ✪ and fertile egg mean densities by ● . 95% confidence limits of the means (± 2 se) are marked * . Both curves are fitted by eye, based on 1363 measurements of eggs of known hatching dates.


1·12
1·04
0·96
0·88
EGG
DENSITY
INDEX
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
DAYS TO HATCHING

seabird populations; i.e. seeking effects of pollution etc. on the population dynamics of seabird colonies. A method has already been described whereby hatching dates can be estimated to ± two or three days, without bias, from egg density. A distribution of hatching dates which is strongly positively skewed would indicate the presence of large numbers of inexperienced pairs (which tend to lay after the median laying date). However, this distribution can also result from the laying of replacement clutches if early laid first clutches are lost.

In the Great Skua clutches measured on Foula in 1975, both egg length and egg breadth declined seasonally in first and second laid eggs in clutches of two, and so therefore did egg volumes (appendix 33), but in single egg clutches the trend was less clear. In 1976, egg volume declined seasonally in single egg clutches, but showed less consistent changes in clutches of two eggs (appendix 34), although eggs hatched after 30 June are clearly smaller than those hatched earlier. These trends also seem to differ between the two seasons, although the reason for such differences is obscure (figure 27). Egg parameters differ little between birds of known ages and birds of unknown (but generally greater) ages, although the youngest birds (six years old), most of which were probably also breeding for the first time, had significantly shorter eggs than birds of unknown age (difference (mean) = 1.52 mm, $t_{343} = 2.77$, $p < 0.01$). The large variation in egg volumes within time intervals, inconsistent differences between time intervals in each season and unexplained differences between seasons do not support the use of egg volumes to investigate age structure of Great Skua colonies.

Figure 27. Seasonal variation of egg volumes in 1975 and 1976 on Foula. Mean volumes of clutches of one egg are marked ● in 1975 and ○ in 1976. First eggs in clutches of two are marked ▼ in 1975 and ▽ in 1976. Second eggs in clutches of two are marked ▲ in 1975 and △ in 1976.


92
90
88
86
84
82
80
78
EGG
VOLUME
(cm3)
5,6
15,6
25,6
5,7
DATE

Chick growth

In 1975, a total of 465 chicks of known hatching date and nest history were available for a study of growth rates. Wing lengths were measured using the maximum chord technique (Spencer 1965) excluding the down on very small chicks, and leg length measured on a straightened leg from the inner angle of the intertarsal joint to the tip of the centre toe nail. Both measurements were always made to the nearest 1 mm. Over the 45 days after hatching, 1740 sets of measurements of weight, wing and leg length were taken. Very few chicks were measured on more than five occasions, and chicks were not remeasured within a period of less than four days, so all sets of measurements have been analysed as if statistically independent. This simplification is unlikely to cause difficulties because of the large sample sizes used in comparisons.

For many successful nests hatching dates were not exactly determined but almost all of these were examined when the chicks had just recently hatched, so it was essential to be able to calculate hatching date from the measurements of these chicks. To do this, measurements of chicks known to be aged 0 - 5 days and of known brood size and hatching order were tabulated, stratified by brood size and hatching sequence. There were no consistent differences which could be related to brood size or hatching sequence between any of the measured parameters (table 85), so discriminant functions were calculated without further consideration of chick status. Although chick weight showed the highest coefficient of variation of the three measurements, it proved to be the best parameter for discriminating between chicks of different ages.

Discriminant funtions classifying chicks into ages 0 - 5 days correctly classified 67.6 % of known age chicks, and these functions

Table 85. Measurements of chicks of known age and status from study nests on Foula in 1975. Wing and leg in mm, weight in g. (Sample sizes for wing and leg measurements the same as for weights).

Parameter and chick category		Age (days after hatching) 0	1	2	3	4	5
WEIGHT (g)							
b/1	n	17	9	7	3	10	4
	mean	64.47	67.67	80.14	105.33	123.20	167.50
	se	1.19	1.58	2.92	2.67	4.15	4.79
	CV	7.6	7.0	9.6	4.4	10.7	5.7
b/2 (first hatched)	n	21	27	16	13	14	13
	mean	66.20	69.60	81.25	97.53	131.50	151.45
	se	0.89	1.17	2.20	2.38	4.15	8.34
	CV	6.0	8.4	10.8	8.8	11.8	18.3
b/2 (second hatched)	n	24	13	13	17	10	14
	mean	66.39	70.23	77.58	97.88	126.00	153.07
	se	0.65	1.33	2.42	3.70	4.99	5.96
	CV	4.7	6.8	10.8	15.6	12.5	14.6
WING LENGTH (mm)							
b/1	mean	24.59	26.00	27.14	29.67	30.30	33.75
	se	0.33	0.44	0.55	1.45	0.42	0.25
	CV	5.6	5.1	5.4	8.5	4.4	1.5

Table 85. Measurements of chick of known age and status from study nests on Foula in 1975. Continued.

Parameter and chick category		Age (days after hatching) 0	1	2	3	4	5
WING LENGTH (mm) Continued							
b/2 (first hatched)	mean	24.14	25.52	26.88	28.15	29.93	32.00
	se	0.41	0.25	0.47	0.41	0.37	0.75
	CV	7.8	5.0	7.0	5.2	4.6	8.4
b/2 (second hatched)	mean	24.79	26.31	26.92	27.68	29.30	31.57
	se	0.33	0.21	0.41	0.35	0.42	0.65
	CV	6.6	2.8	5.5	5.5	4.6	7.7
LEG LENGTH (mm)							
b/1	mean	52.82	57.11	59.00	65.67	67.70	73.25
	se	0.39	0.51	0.95	0.88	0.80	1.11
	CV	3.1	2.7	4.2	2.3	3.8	3.0
b/2 (first hatched)	mean	52.29	56.15	59.56	62.85	68.00	72.54
	se	0.57	0.29	0.39	0.60	0.80	1.56
	CV	5.0	2.7	2.6	3.4	4.4	7.7
b/2 (second hatched)	mean	51.92	56.69	58.54	62.89	67.80	71.43
	se	0.52	0.38	0.59	0.59	0.92	1.24
	CV	5.0	2.4	3.7	4.1	4.3	6.5

were based principally on chick weights. As chicks gain very little weight in the first 48 hours after hatching (table 85) this discriminatory ability can be improved by using two sequential sets of discriminant functions. The first classified chicks into ages 0 days old or at least one day old, using leg length as the main character. The second classified chicks older than 0 days into one, two three four or five or more days old. The use of these two sets of functions (table 86) correctly classified 70.45 % of the known age chicks, with only 0.81 % incorrectly classified by more than one day (table 87).

These discriminant functions were used to determine hatching dates of nests which had not been visited during the hatching process.

In many birds it is found that late hatching chicks have the poorest food supply and early hatched chicks the best (Lack 1966); this also appears to be the norm for Foula Great Skuas (section 4). Studies of southern hemisphere skuas have shown that second hatched chicks in broods of two frequently starve to death (Young 1963, Reid 1967), so comparing the growth of single chicks hatched early in the season, should show most clearly any differences to be found as a result of variations in food availability. As is usual (Ricklefs 1973) growth of leg and wing are less variable than growth in terms of weight (figures in appendix 35). Thus any detectable variations in growth rate in relation to brood size, hatching sequence or hatching date should be most easily seen in chick weight measurements. For this reason weights of chicks of known age and status were first examined. The mean weight of all chicks at each day of age was tabulated (appendix 36) then the deviations of chicks of given brood size, sequence and hatching date from these means were calculated (figures 28, 29 and 30).

Two consistent patterns can be seen in figures 28 to 30.

Table 86. Discriminant functions used to age small chicks from their measurements.

Ages discriminated	variable	change in Rao's V	significance of change in V	unstandardised function coefficients	
				1	2
0 with 1 +	leg length	116.02	$p < 0.001$	0.32508	-
	weight	3.05	$p = 0.081$	0.02496	-
	constant			- 19.27884	-
				(df 2)	
				(X^2 79.73)	
				($p < 0.001$)	
1, 2, 3, 4, 5 +	weight	1008.51	$p < 0.001$	0.02621	0.10308
	leg length	27.12	$p < 0.001$	- 0.03362	0.15691
	wing length	15.71	$p = 0.003$	0.03244	- 0.61854
	constant			- 3.76264	24.01808
				df 12	6
				X^2 361.80	18.52
				$p < 0.001$	$= 0.005$

Table 87. Ages of chicks estimated from measurements using discriminant functions compared with actual ages.

Actual age (days)	number of cases	correctly aged	one day out	two days out	Age predicted by functions (days) 0	1	2	3	4	5
0	62	51	11	0	51	11				
1	49	33	16	0	5	33	11			
2	36	20	16	0		11	20	5		
3	35	25	10	0			6	25	4	
4	34	21	13	0				7	21	6
5	31	24	5	2				2	5	24
	247	174	71	2						
	100.00 %	70.45 %	28.74 %	0.81 %						

Figure 28. Percentage deviations of chick weights in broods of one chick, from the overall mean weights for each day of age, when chicks are divided into hatching periods: 1.6 to 10.6 (▲), 11.6 to 15.6 (□), 16.6 to 20.6 (■), 21.6 to 25.6 (o), and 26.6 to 20.7 (●). Deviations which differ significantly from zero ($p < 0.05$) are marked * .

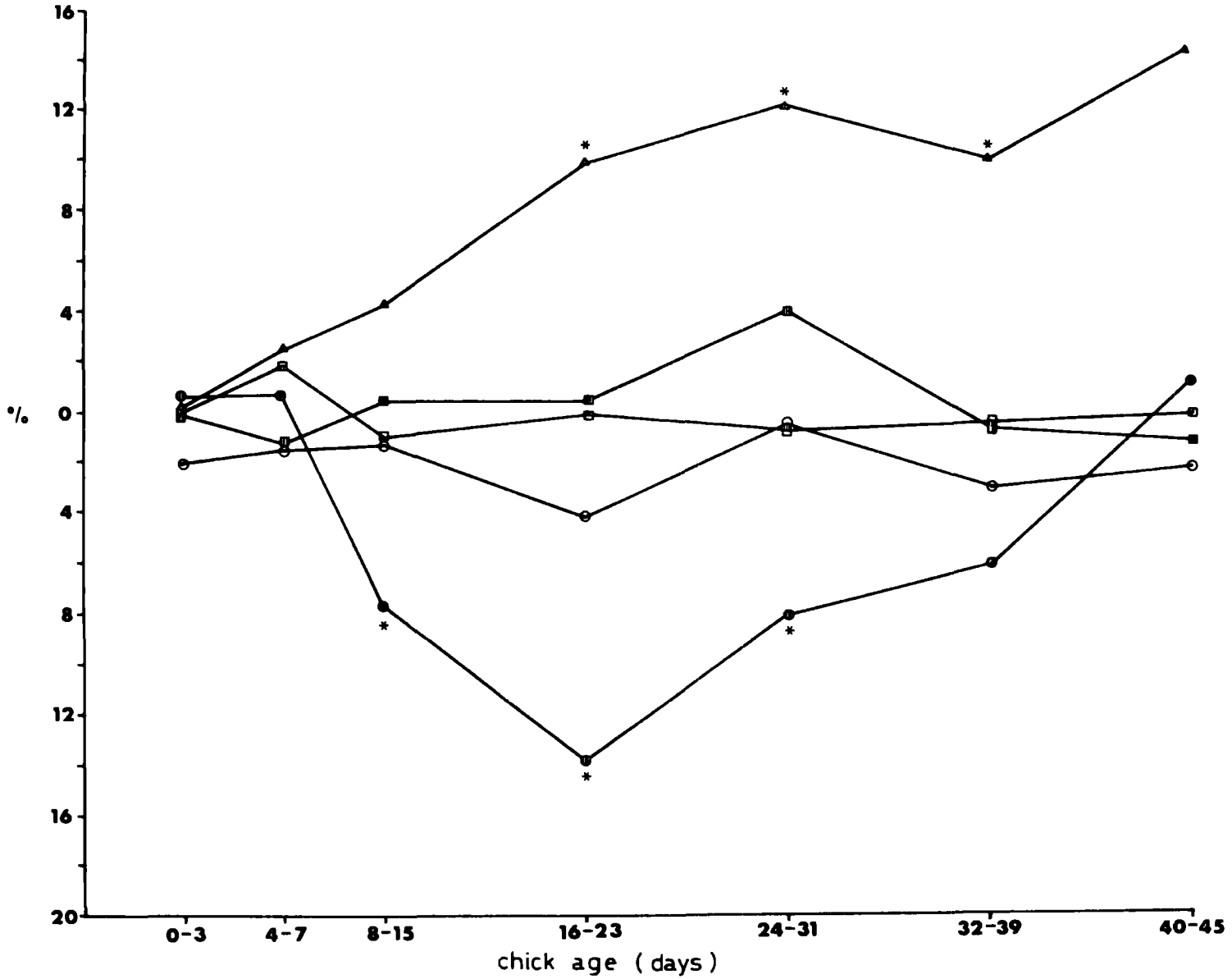

16
12
8
4
0
4
8
12
16
20
%
0-3
4-7
8-15
16-23
24-31
32-39
40-45
chick age (days)

Figure 29. Percentage deviations of chick weights in first hatched of broods of two chicks from the overall mean weights for each day of age. Hatching periods and symbols are as in figure 28.

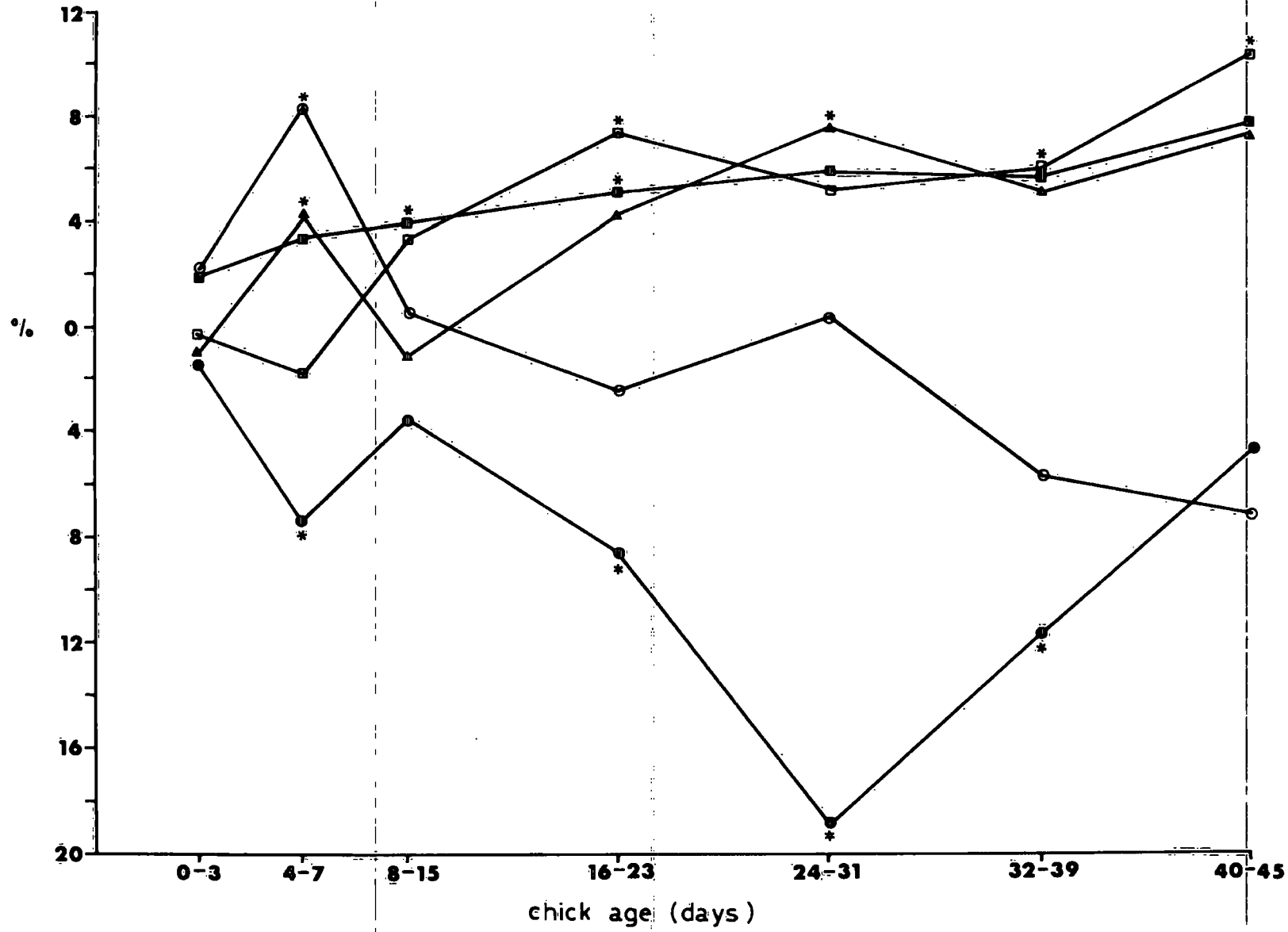
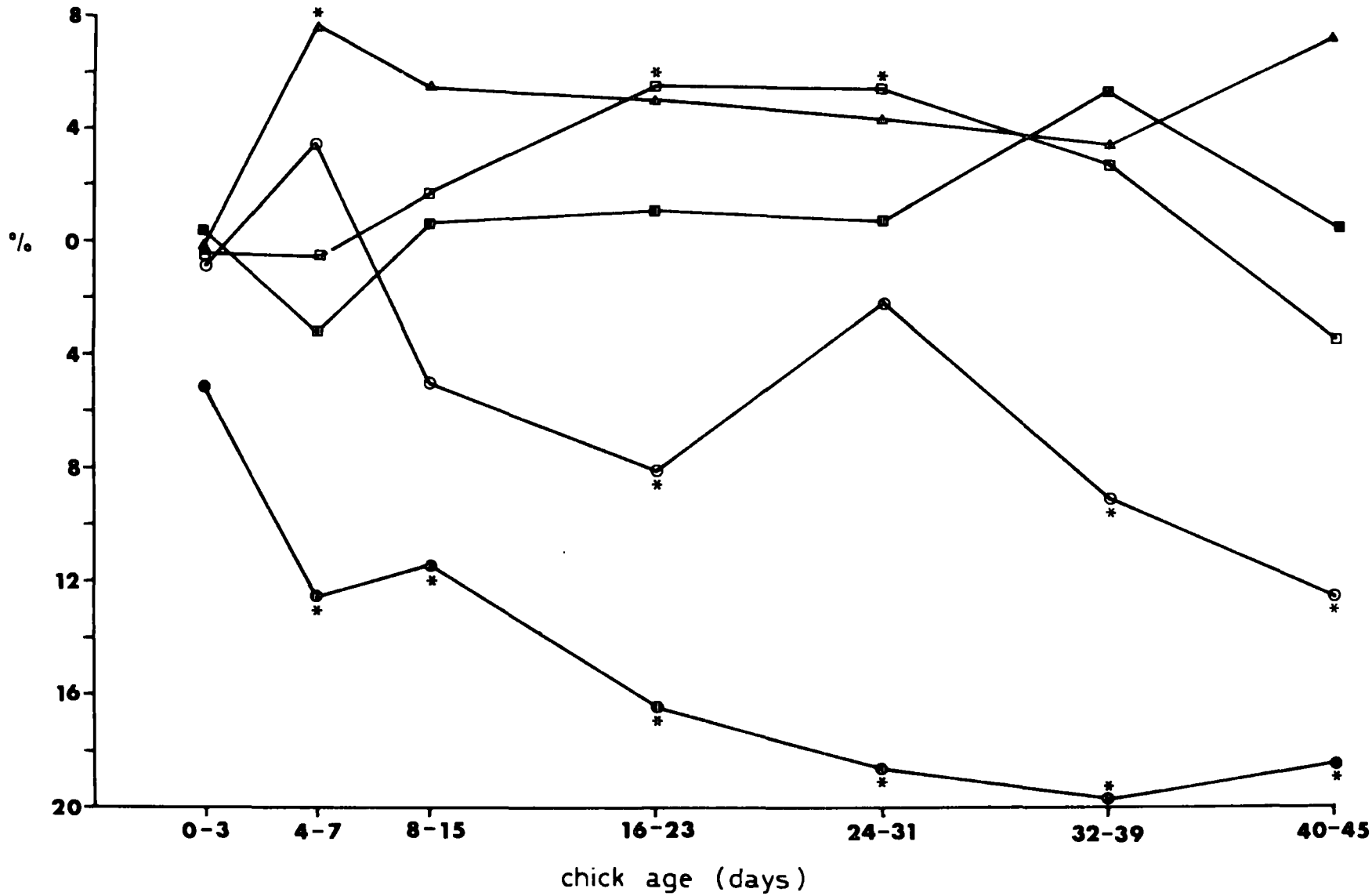

12
8
4
0
4
8
12
16
20
%
0-3
4-7
8-15
16-23
24-31
32-39
40-45
chick age (days)

Figure 30. Percentage deviations of chick weights in second hatched of broods of two chicks from the overall mean weights for each day of age. Hatching periods and symbols are as in figure 28.


8
4
%
0
4
8
12
16
20
0-3
4-7
8-15
16-23
24-31
32-39
40-45
chick age (days)

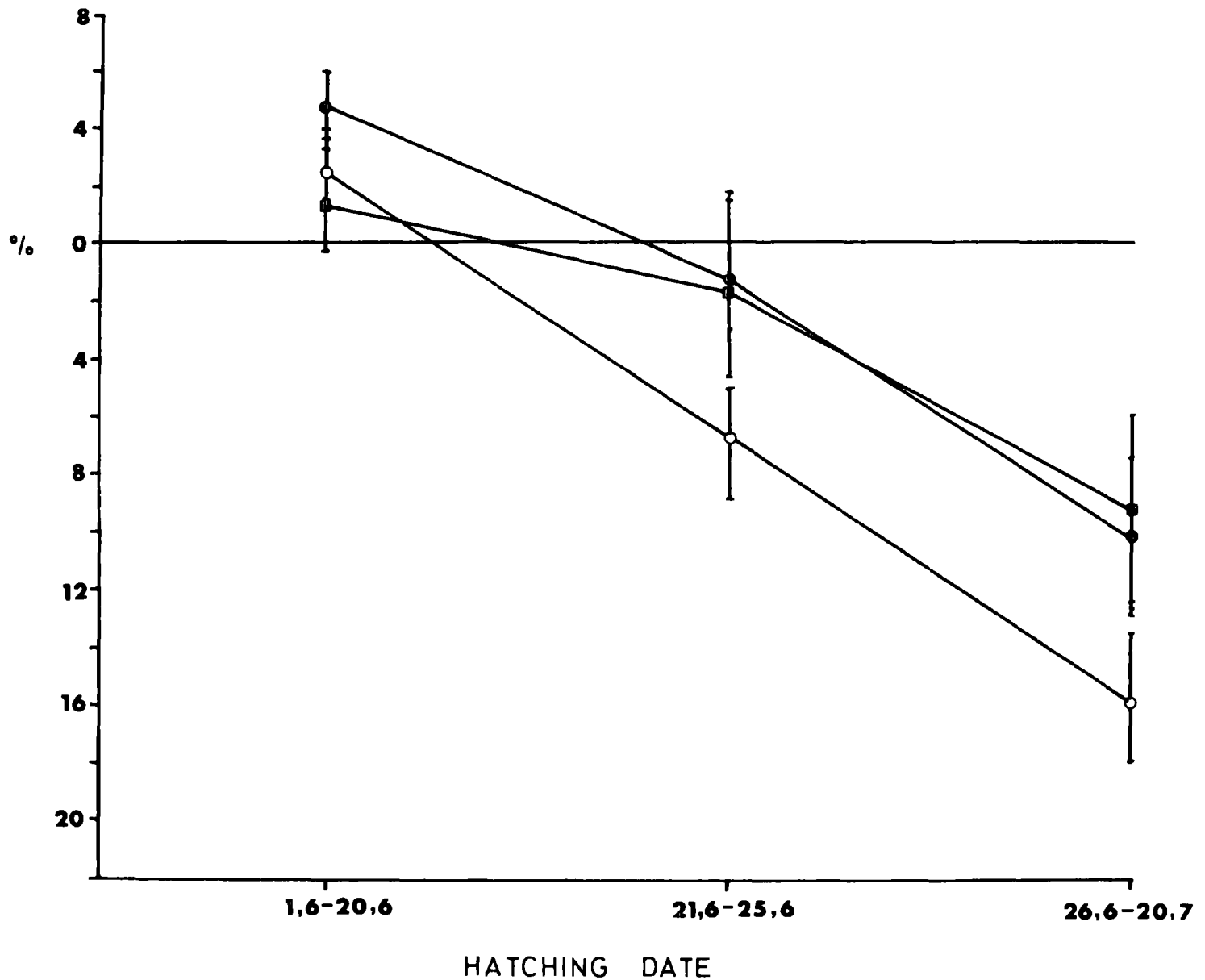
The deviations from mean weight tend to be positive for early hatched, and negative for late hatched chicks, as predicted earlier, and the deviations, particularly negative ones, tend to be most pronounced between the eighth and 39th days after hatching. This coincides with the period of most rapid weight gain; when heavy chicks cease to gain weight (at about 40 days) the underweight chicks may catch up by continuing to gain weight.

With the exception of the small number of single chick broods hatched before 1 June, there are no significant differences within chick-status categories between weight deviations of chicks hatched in the time periods up to 20 June, but deviations from mean weights differ significantly between these chicks and those hatched between 21 June and 25 June, and both these groups differ significantly from those hatched after 25 June (table 88 and figure 31).

Table 88. Deviations of chick weights from the mean when tabulated into brood categories and hatching periods. Only chicks aged between 8 and 39 days are included (see text).

		Brood category		
Hatching period	statistic	b/1	b/2 1st hatched	b/2 2nd hatched
1 June to 20 June	sample size	165	322	268
	deviation (%)	+ 1.32	+ 4.78	+ 2.73
	(se)	0.70	0.50	0.55
21 June to 25 June	sample size	45	46	38
	deviation (%)	- 1.78	- 1.44	- 6.59
	(se)	1.34	1.33	1.46
26 June to 20 July	sample size	46	67	57
	deviation (%)	- 9.25	- 10.09	- 15.68
	(se)	1.33	1.10	1.19

Figure 31. Percentage deviations of weights of chicks aged between 8 and 39 days from the mean weights of all chicks measured on Foula in 1975 for every day of age. Mean deviations of chicks in broods of one (■), first hatched (•) and second hatched (o) of broods of two are shown for chicks hatched early (1.6 to 20.6), late (21.6 to 25.6) and very late (26.6 to 30.7). 95 % confidence intervals of the means (± 2 se) are shown by bars.


8
4
%
0
4
8
12
16
20
1,6-20,6
21,6-25,6
26,6-20,7
HATCHING DATE

Single chicks show a significantly smaller positive weight deviation than first hatched chicks in broods of two during the first hatching period, which might be due to greater stimulation of two begging chicks resulting in the larger chick obtaining more food than if alone, but the difference is very small. It is therefore convenient to group together all chicks hatched before 21 June, regardless of brood status, and consider these to exhibit "typical" growth. Deviations of late hatched chicks may then be expressed relative to these "typical" chicks.

Late hatched second chicks fall further below typical weight than either single chicks or first hatched chicks, while these last two categories do not differ significantly (table 89). Deviations of wing length measurements are smaller, but follow the same trends as weight, and deviations of leg measurements are smaller still, but again show the same trends as weights.

While second chicks hatched after 25 June have fallen behind by the equivalent of 3.5 days growth in weight, they are only 1 day behind in wing growth, and only 0.6 days behind in leg growth when compared with "typical" chicks, so wing and leg measurements will provide reasonable measures of chick age even when chicks have been undernourished. By ageing chicks from their wing lengths, their weights can be compared with the expected "typical" weight for that age, giving an index of food availability measured in terms of chick body condition.

"Typical" growth data are given in appendix 37 and in figures 32, 33 and 34. Using the methods of Ricklefs (1967) a logistic curve was fitted to the weight data for typical growth. The equation is:

$$W(g) = \frac{1167.075}{1 + 16.955\, e^{-0.176\, t}}$$

Table 89. Deviations of late hatched chicks from "typical" growth. Deviations are expressed as a percentage of the "typical" mean. Standard errors are given in parentheses.

Hatching period.	Statistic	Brood category b/1	b/2 1st hatched	b/2 2nd hatched
1 June to 20 June	sample size	165	322	268
21 June to 25 June	sample size	45	46	38
	weight	- 5.28 (1.34)	- 4.94 (1.33)	- 10.99 (1.46)
	wing	+ 1.27 (0.80)	+ 3.40 (0.67)	+ 4.62 (0.79)
	leg	- 0.98 (0.34)	- 0.20 (0.30)	- 1.89 (0.40)
26 June to 20 July	sample size	46	67	57
	weight	- 12.75 (1.33)	- 13.59 (1.10)	- 19.18 (1.19)
	wing	- 5.48 (0.87)	- 6.14 (0.78)	- 9.82 (0.94)
	leg	- 2.55 (0.61)	- 1.71 (0.26)	- 3.78 (0.42)

Figure 32. Chick weights at each day of age from hatching to fledging, for chicks hatched before 20 June on Foula in 1975 (defined as typical growth). Mean weights are marked ● and 66% confidence limits for individual weights (mean ± 1 standard deviation) are marked * . The superimposed curve is the best logistic fit:

$$W = \frac{1167.075}{1 + 16.955e^{-0.176t}}$$

where W is chick weight (g) and t is chick age in days from hatching.

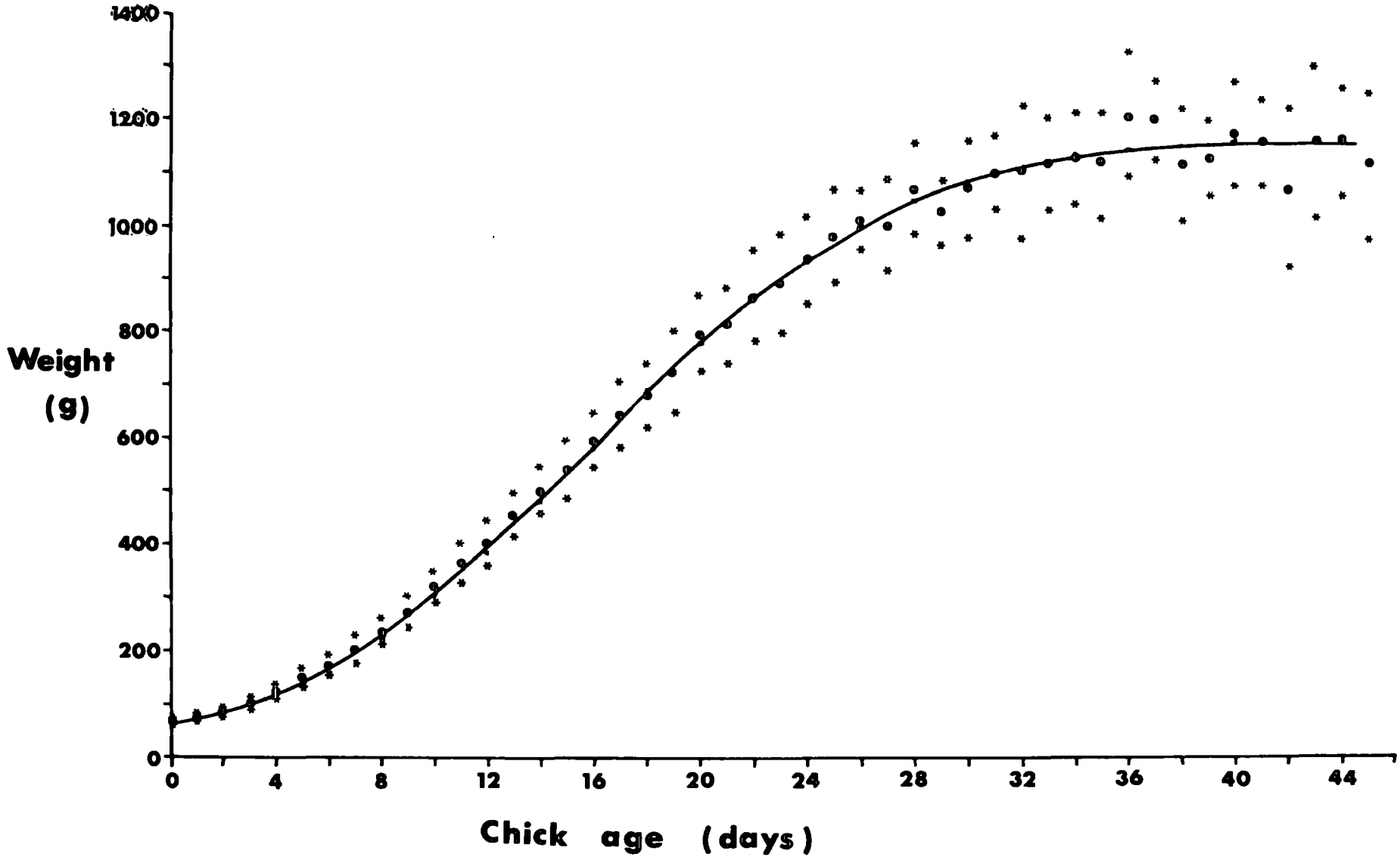

1400
1200
1000
800
600
400
200
0
Weight
(g)
0
4
8
12
16
20
24
28
32
36
40
44
Chick age (days)

Figure 33. Chick wing lengths (maximum chord in mm.) at each day of age from hatching to fledging, for chicks hatched before 20 June on Foula in 1975. Mean wing lengths are marked • and 66% confidence limits for individual wing lengths (mean ± 1 S.D.) by * .

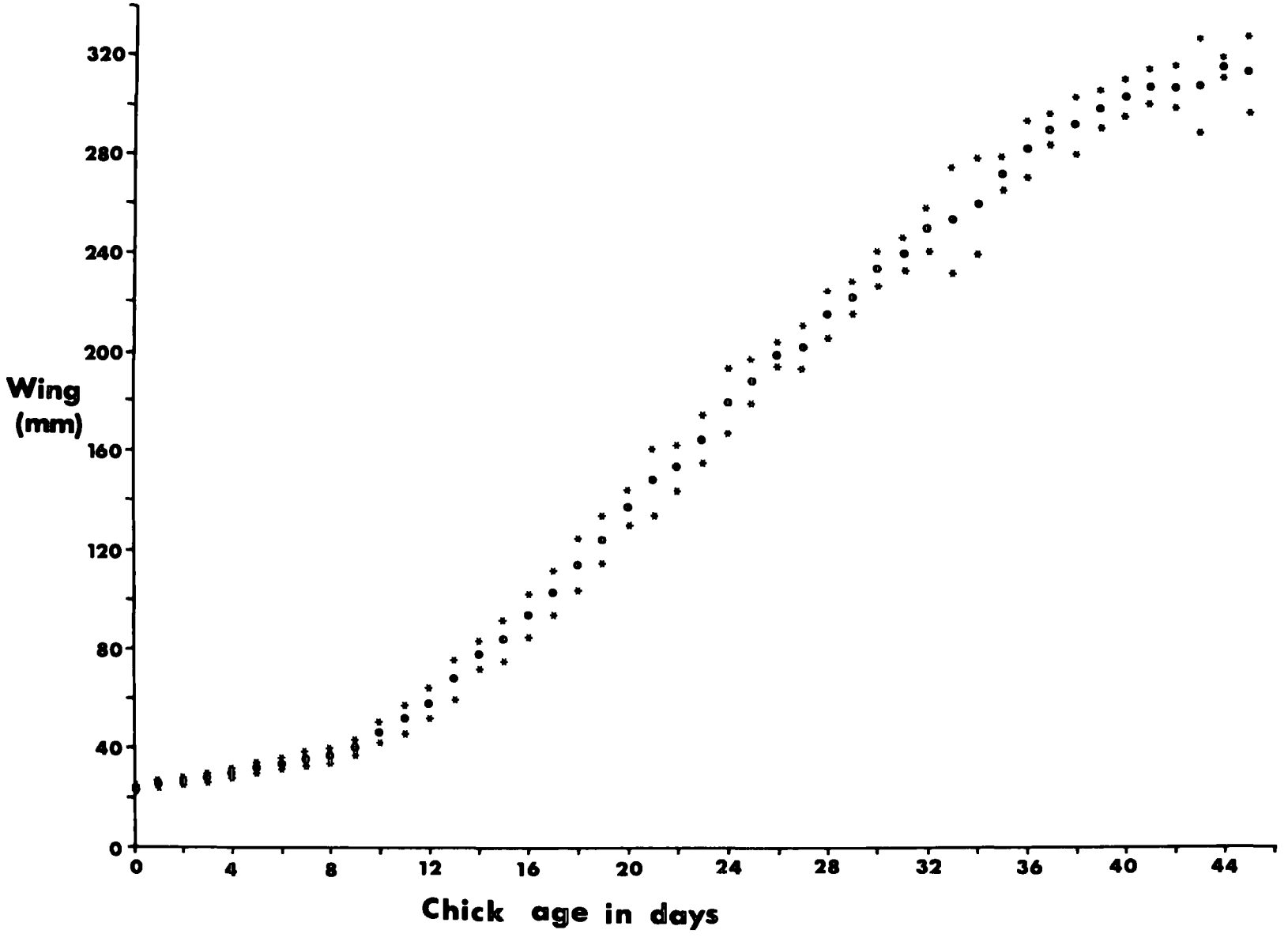
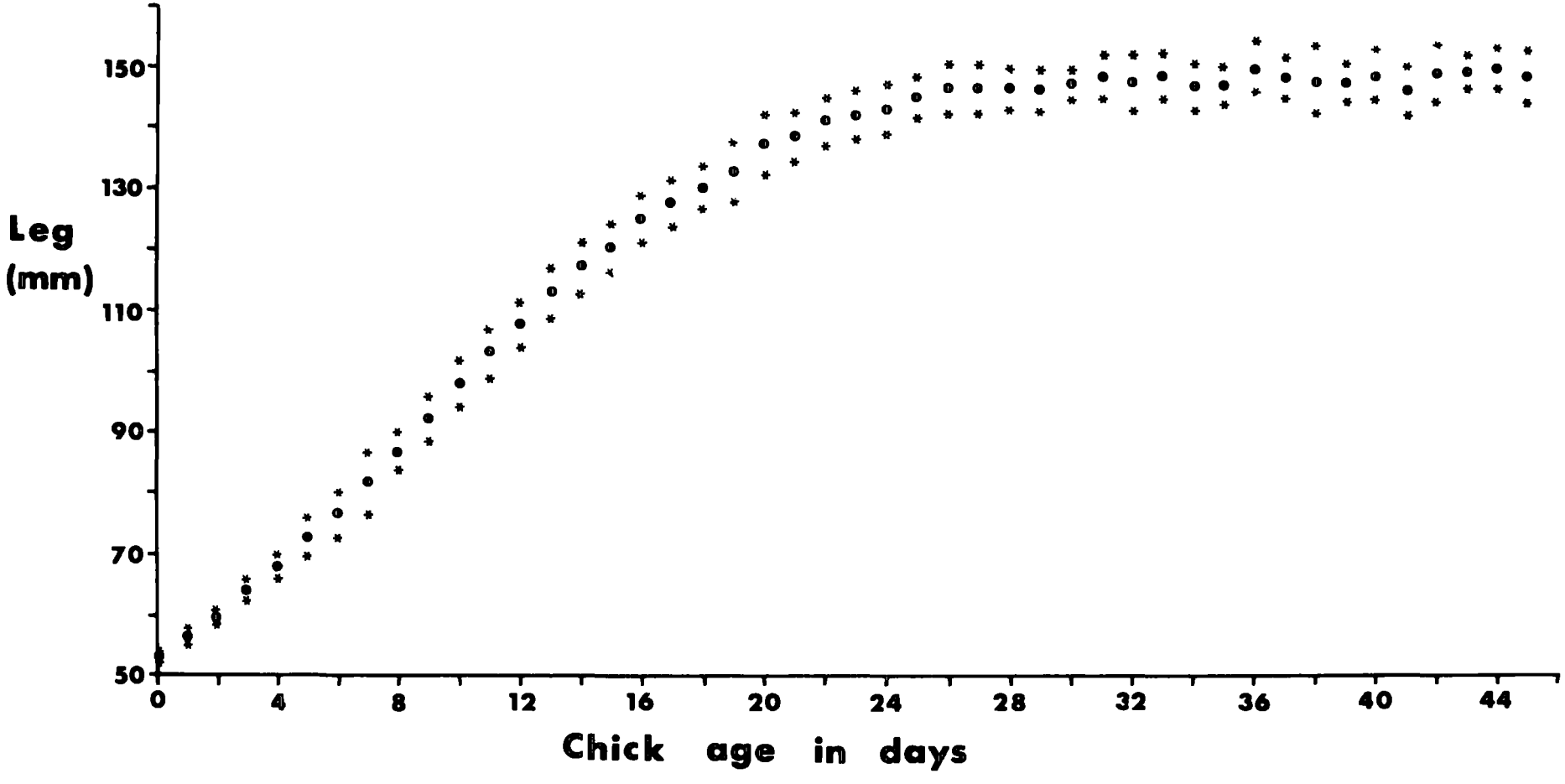

Wing
(mm)
320
280
240
200
160
120
80
40
0
0
4
8
12
16
20
24
28
32
36
40
44
Chick age in days

Figure 34. Chick leg lengths at each day of age from hatching to fledging, for chicks hatched before 20 June on Foula in 1975. Mean leg lengths are marked ● and 66% confidence limits for individual leg lengths (mean $\pm$ 1 S.D.) by * .


Leg
(mm)
150
130
110
90
70
50
0
4
8
12
16
20
24
28
32
36
40
44
Chick age in days

where W is the chick weight (g) and t is the age of the chick in days after hatching. This curve is superimposed on the observed weight data in figure 32.

Chicks growing "typically" can be accurately aged from their weight only when less than 500 g (about 14 days old) (Appendix 38). At any age, undernourished chicks will be seriously under-aged from their weight, so I have used weight only to help to age chicks less than one week old. Leg length allows chicks to be aged to 2 days (2 standard deviations) when leg length is less than 120 mm, after which leg growth slows rapidly, giving low ageing accuracy (Appendix 39). Wing length gives an accurate measure of chick age almost to fledging size (Appendix 40), although accuracy decreases slightly when chicks exceed 35 days old.

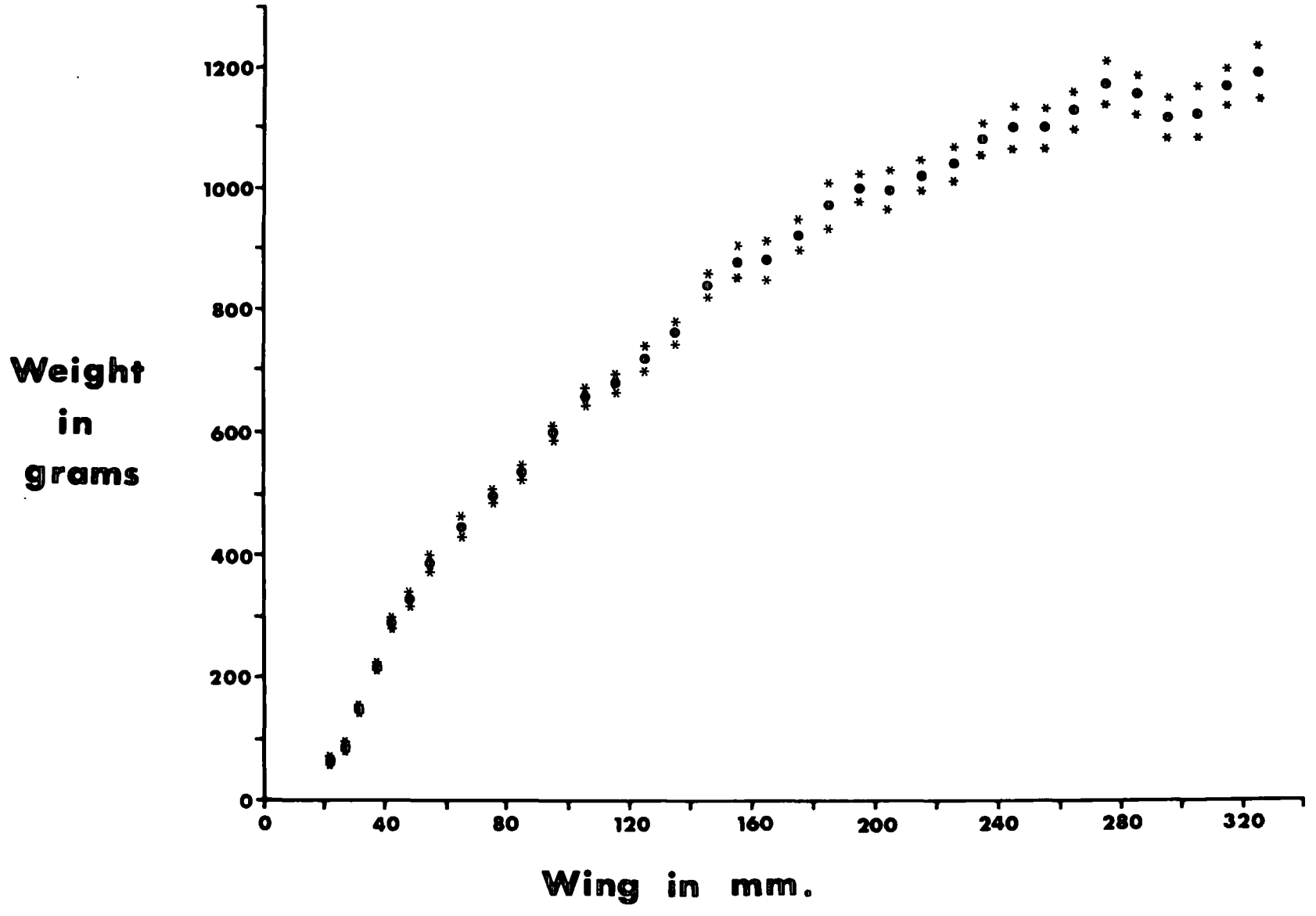
The conversion tables to give chick ages from measurements are given in appendixes 41 and 42.

Again using only chicks hatched before 20 June, typical weights of chicks of particular wing lengths were calculated. These follow a smooth curve (figure 35), against which observed weights of chicks measured in other seasons or at particular dates can be compared (appendix 43) to determine whether chick growth is influenced by variations in food availability during and between seasons. Brathay expeditions have weighed and measured all Great Skua chicks ringed on Foula each season since 1973, and these studies of typical chick growth will allow their data to be analysed.

Pesticides, pollutants and reduced breeding success

Seabirds may accumulate high concentrations of Dieldrin (Robinson et al. 1967, Stickel et al. 1969, Coulson et al. 1972), DDE (Braestrup

Figure 35. The relationship between weight and wing length for Great Skua chicks hatched before 20 June on Foula in 1975. Mean weights are marked • and 95% confidence limits for the means (± 2 se) are marked * .


Weight in grams
1200
1000
800
600
400
200
0
0
40
80
120
160
200
240
280
320
Wing in mm.

et al. 1974, Jorgensen & Kraul 1974), PCBs (Jensen et al. 1969, Prestt et al. 1970, Bourne & Bogan 1972, Zitko et al.1972, Gilbertson & Reynolds 1974), mercury (Keckes & Miettinen 1970, Vermeer 1971, Dale et al. 1973) and cadmium (D. Osborn in litt.). At sufficiently high concentrations these substances may cause death, and at sub-lethal concentrations may reduce breeding success (Ratcliffe 1967, Heath et al. 1969, Hays & Risebrough 1972, Peakall 1972, Gress et al. 1973, Koeman et al. 1973, Longcore & Samson 1973, Platnow & Reinhart 1973, Stickel 1973, Tumasonis et al. 1973, Blus et al. 1974, Heinz 1975), although mechanisms and effects differ between pollutants and between species (Anderson et al. 1969, Heath et al. 1972, Haegele & Tucker 1974, Jorgensen & Kraul 1974, Scott et al. 1975).

Animals high up food webs tend to hold highest concentrations of pollutants. The surface of the ocean is enriched with PCB relative to subsurface waters (Bidleman & Olney 1974) so PCB is accumulated particularly in pelagic surface feeding organisms. The Great Skua combines all the traits favouring accumulation of PCBs. It preys on other seabirds, feeds on the ocean surface and it wanders the open North Atlantic in winter rather than moving to a less contaminated environment. High concentrations of cadmium are also associated closely with pelagic habits (D. Osborn in litt.). In contrast, contamination with Dieldrin, DDE and mercury is highest in birds of inshore areas of industrial activity (Sproul et al. 1975) although even skuas breeding in the Antarctic contain detectable concentrations of organochlorines (Tatton & Ruzicka 1967).

The concentrations of Dieldrin, DDE, and PCBs in Great Skua tissues and eggs have been determined in small samples from Handa (Prestt et al. 1970), Shetland (Bourne & Bogan 1972) and Iceland (Sproul et al. 1975). A sample of 12 eggs from 12 clutches was taken

from Foula in 1976 and sent to Shell (Sittingbourne) for analysis of organochlorine concentrations; samples from these eggs were analysed for mercury and cadmium by M. Hutton, Chelsea College. Eleven Great Skuas of known ages between 3 and 12 years were collected and tissue samples from these were also analysed to determine mercury and cadmium levels.

The concentrations of cadmium in kidney tissues of Foula Great Skuas (table 90) are the highest yet found in any living vertebrate, and would be lethal to mammals (Flick et al. 1971), but seabirds appear to bind cadmium to protein in a harmless form, and these high concentrations are now thought to be natural and not an effect of pollution (D. Osborn in litt.). Cadmium appears to enter eggs only in minute amounts (table 91).

Mercury levels in adult Great Skua tissues are considerably higher than usually found in pelagic birds (usually below 6 ppm dry weight) but below levels recorded in some estuarine ducks or herons (Dale et al. 1973). The maximum level is still well below experimentally determined lethal concentrations (Fimreite & Karstad 1971, Koeman et al. 1971, Borg et al. 1969, Borg et al. 1970) but may be sufficiently high to cause a decrease in egg hatchability. Eggs normally contain between a fifth and a ninth of the liver concentration of the mother (Fimreite et al. 1970) which could be as much as 6 ppm dry weight (i.e. 1.7 ppm wet weight) based on data in table 90. Actual mercury concentrations in eggs ranged up to 1.311 ppm wet weight on only a sample of five (table 91), while Borg et al. (1969) and Fimreite (1971) reported decreased hatchability of pheasant's eggs containing 1.3 - 2.0 ppm and 0.5 - 1.5 ppm wet weight respectiviely. In contrast, Vermeer et al. (1973) found that concentrations of mercury of between 2 and 16 ppm wet weight in Herring Gull eggs did not result in

Table 90. Concentrations of cadmium and mercury in liver and kidney of adult Great Skuas on known age collected on Foula in 1976.

Age of bird	cadmium concentration (ppm dry weight)		mercury concentration (ppm dry weight)	
	liver	kidney	liver	kidney
3	8.8	64.6	15.0	10.4
4	6.8	-	3.2	-
4	1.0	13.5	6.3	7.9
5	4.3	52.6	4.9	4.9
5	-	14.5	-	10.1
7	8.2	129.2	6.5	4.2
7	1.9	21.6	27.6	18.6
8	1.8	29.7	3.6	6.1
9	10.8	114.7	9.6	6.3
10	4.4	91.2	9.3	19.5
12	31.4	336.0	30.4	-
Geometric means	5.0	53.5	8.7	8.5

Footnote: tissues were freeze dried so that wet weight concentrations are approximately given by

$$\frac{\text{ppm dry weight}}{3.5}$$

Table 91. Concentrations of heavy metals in Great Skua eggs analysed for organochlorine residues (table 93).

egg number	cadmium concentration (ppm wet weight)	mercury concentration (ppm wet weight)
1	0.022	0.275
2	none detected	0.284
3	0.016	0.409
4	none detected	1.311
5	0.012	0.575

hatching failure. Fimreite (1974) found that the mercury concentration in Common Tern eggs which had failed to hatch in a colony with severely reduced breeding success averaged 3.65 ppm while another colony with normal breeding success averaged 1.00 ppm in a sample of eggs containing embryos. Clearly sensitivity to mercury varies greatly between species but the levels in Great Skua eggs are probably just below that required to impair breeding. Such high levels of mercury in Great Skuas were unexpected and contrast with levels in other pelagic seabirds. The reason for this is obscure. Although very variable, there is a suggestion in the data that both cadmium and mercury levels are highest in the oldest birds sampled. Higher levels might be found in older individuals but no older ringed birds are present to examine.

Organochlorine levels in muscle or egg show PCBs to be present in large amounts but, as expected, DDE and particularly Dieldrin are at relatively low concentrations (tables 92 and 93). Sproul et al. (1975) found that Great Skuas contained much higher concentrations of PCBs and DDE than any other Icelandic seabirds and suggested that levels might be sufficiently high to impair reproduction. Levels in British Great Skuas appear to be very similar to those found in Iceland, although levels in eggs from Foula in 1976 appear to be lower than those found in 1971 to 1973 (tables 92 and 93) and this might reflect reduced use of PCB and DDT in recent years which has resulted in a detectable decrease in residue levels of PCBs in North Atlantic surface water (Harvey et al. 1974) and of Dieldrin and DDE in Shag eggs in North-east England (Coulson et al 1972).

The Brown Pelican, a particularly sensitive species, suffered a severe reduction in breeding success when the geometric mean PCB level in eggs was 5.50 ppm wet weight and DDE was 1.77 ppm wet weight

Table 92. Organochlorine levels in Great Skua muscle and eggs collected from Britain and Iceland between 1971 and 1973.

Source	Locality	Tissue	Compound	Sample size	ppm wet weight. range	ppm wet weight. geometric mean
Bourne & Bogan (1972)	Shetland (1971, 72)	Muscle	DDE	5	2.2 - 4.0	2.8
			PCB	5	10.2 - 32.0	15.9
Sproul et al. (1975)	Iceland (1973)	Muscle	Dieldrin	10	0.047 - 0.350	0.12
			DDE	10	1.8 - 12.0	4.4
			PCB	10	5.3 - 47.0	16.0
		Egg	Dieldrin	13	arithmetic mean of	0.20
			DDE	13	arithmetic mean	5.9
			PCB	13	arithmetic mean	27
Prestt et al. (1970)	Handa (1969)	Egg	PCB	1		25

Table 93. Concentrations of organochlorines in Great Skua eggs collected on Foula in 1976.

Egg number	Concentration of organochlorine in ppm wet weight					
	PCB (as Aroclor 1262)	pp DDE	pp DDD	pp DDT	Dieldrin	HCB
1	19	1.7	0.04	0.12	0.16	0.04
2	13	1.1	0.05	0.16	0.092	0.04
3	9.7	1.6	0.05	0.22	0.073	0.03
4	33	3.2	0.07	0.22	0.088	0.09
5	10	1.2	0.04	0.10	0.079	0.03
6	36	3.6	0.07	0.28	0.15	0.16
7	19	2.5	0.10	0.55	0.089	0.07
8	30	1.7	0.05	0.24	0.086	0.06
9	13	1.4	0.04	0.15	0.056	0.05
10	6.1	0.43	0.03	0.05	0.022	0.03
11	33	3.2	0.04	0.27	0.096	0.07
12	21	1.7	0.11	0.56	0.097	0.08
Geometric means	17.6	1.70	0.053	0.199	0.082	0.055

in successful nests and PCB was 7.94 and DDE 3.23 ppm in unsuccessful nests (Blus et al. 1974), but Herring Gulls in the Baltic Sea had an average of 92 ppm PCB and 57 ppm DDE but were reproducing normally (Koeman et al 1973). Whether PCB and DDE levels now found in Great Skuas impair breeding will depend on the sensitivity of this species to these compounds.

Shell thinning appears to be caused by DDE but not by PCBs, and becomes evident at DDE concentrations below those which impair reproduction but which depend on the sensitivity of the species (Blus et al. 1971, Stickel 1973). Sproul et al. (1975) found no differences in shell thicknesses or Ratcliffe index between 30 Icelandic Great Skua eggs collected before 1947 and 12 collected in 1973. Ratcliffe indexes (Ratcliffe 1967) were calculated for all North Atlantic Great Skua eggs held in the British Museum (Tring), all of which had been collected before 1930. There were slight differences between measurements of Iceland, Faroes and Shetland eggs, but no evidence of eggshell thinning when these indices were compared with those of eggs collected on Foula in 1976 (table 94). This implies that the current DDE level in Great Skuas is not likely to be having harmful effects on reproduction.

The main sublethal effect of PCBs is a reduction of egg hatchability. Egg fertility is unaffected, and most embryonic mortality occurs during the hatching process (Scott et al. 1975). Heath et al. 1972 found no significant effect on reproduction when Mallards were fed Aroclor 1254 for two years at a dose of 25 ppm in the diet. This dose resulted in concentrations of 33 and 56 ppm PCB in two eggs from treated birds; levels slightly greater than detected in most of the Great Skua eggs sampled. In contrast, Ring Doves laying eggs containing only 16 ppm PCB suffered a 60% decline in hatchability relative to

Table 94. Ratcliffe index values for Great Skua eggs in British Museum (Tring), from Foula, Shetland in 1976, and reported by Sproul *et al.* (1975)

Period of collection	Category	sample size	Ratcliffe index	
			mean	standard error
pre 1940 (BMNH)	Iceland	30	1.776	0.027
pre 1940 (BMNH)	Faroe	58	1.664	0.018
pre 1940 (BMNH)	Shetland	59	1.739	0.015
1976 (Foula)	c/1	5	1.705	0.034
1976 (Foula)	c/2 (first laid)	43	1.775	0.017
1976 (Foula)	c/2 (second laid)	47	1.761	0.019
pre 1947 (Sproul *et al.*)	Iceland	30	1.75	0.04
1973 (Sproul *et al.*)	Iceland	12	1.76	-

controls (Peakall & Peakall 1973). Scott et al. (1975) found that a diet containing Aroclor 1248 was much more toxic than one containing the same amount of Aroclor 1254 or 1260, so it is difficult to predict the effect of a particular level of PCB both because species sensitivity varies greatly and because isomer toxicity varies. However, it could be predicted that the high level in Great Skuas would, if the species is sensitive to PCBs, result in abnormally high embryonic mortality at hatching, and possibly in gross deformity of embryos (Tumasonis et al. 1973).

The fates of Great Skua eggs in marked-nest studies were recorded on Foula and by Fair Isle Bird Observatory (table 95). The high proportion of "addled" eggs, expressed as a percentage of all eggs surviving the normal period of incubation, the high proportion of embryos which died during hatching, expressed as a percentage of all eggs with embryos which survived up to hatching, and the occurrence of six deformed chicks of 1403 hatched indicated that PCB or mercury levels might be affecting Great Skua reproduction. Similar studies of a range of seabird species, where there was no indication of pollutant or pesticide influence, are listed in table 96.

Division of the species in table 96 into three categories: skua species, "other Larinae" and "other seabirds" did not show any significant differences in the proportion of addled eggs between categories ($X^2_2 = 0.949$, ns) while the number of embryos which died hatching were too small to compare statistically. However, comparing the totals for each table, Shetland Great Skuas showed twice as many addled eggs, and eight times as many deaths at hatching as were found in the other studies combined. Both differences are highly significant ($X^2_1 = 167.4$, $p < 0.001$ and $X^2_1 = 125.3$, $p < 0.001$).

Table 95. Fate of Great Skua eggs in marked-nest studies on Foula and on Fair Isle (1957 data from Williamson (1957) and 1974-76 data from R.A. Broad in litt.) (% addled is % of eggs surviving incubation period; % died hatching is % of embryos which survived to hatching - see text).

Area	Year	eggs laid	eggs lost	addled eggs	Percent addled	died hatching	% died hatching	hatched deformed
Foula; Ristie	1973	21	2	3	15.8	0	0.0	0
Foula; Ristie	1974	39	11	9	32.1	2	10.5	0
Foula; Ristie	1975	60	6	16	29.6	2	5.3	0
Foula; Ristie	1976	60	3	13	22.8	1	2.3	0
Foula; Flick	1973	225	69	24	15.4	7	5.3	0
Foula; Flick	1975	344	110	31	13.3	8	3.9	4
Foula; East	1975	487	53	73	16.8	6	1.7	2
Foula; East	1976	718	44	116	17.2	17	3.0	0
Fair Isle	1957	20	2	6	33.3	0	0.0	0
Fair Isle	1974	30	2	7	25.0	1	3.6	0
Fair Isle	1975	40	11	10	34.5	1	5.3	0
Fair Isle	1976	45	12	7	21.2	1	3.8	0
All Shetland		2089	325	315	17.86	46	3.17	6

Table 96. Fate of eggs in marked-nest studies of seabirds.

Species	Authority	eggs laid	eggs lost	eggs left	addled eggs number	addled eggs %	died hatching number	died hatching %
Brown Skua	Burton (1968)	127	35	92	11	12.0	2	2.5
Brown Skua	Stonehouse (1956)	20	9	11	1	9.1	0	0.0
South Polar Skua	Young (1963)	94	10	84	6	7.1	0	0.0
Arctic Skua	Kinnear (1974)	102	31	71	3	4.2	1	1.5
Herring Gull	Paynter (1949)	247	51	196	13	6.6	7	3.8
Herring Gull	Paludan (1951)	641	142	499	44	8.8	6	1.3
Herring Gull	Harris (1964)	610	173	437	45	10.3	3	0.8
Herring Gull	Brown (1967)	250	32	218	52	23.8	0	0.0
Herring Gull	Parsons (1971)	-	-	3277	314	9.6	0	0.0
Herring Gull	Drent (1970)	350	66	284	48	16.9	6	2.5
Lesser Black-backed Gull	Harris (1964)	212	62	144	3	2.1	1	0.7
Lesser Black-backed Gull	Brown (1967)	779	160	619	58	9.4	0	0.0
Kittiwake	Maunder & Threlfall (1972)	-	-	176	11	6.2	3	1.8
Arctic Tern	Langham (1968)	96	20	76	6	7.9	0	0.0
Common Tern	Langham (1968)	580	55	525	10	1.9	7	1.3
Sandwich Tern	Langham (1974)	-	-	1982	85	4.3	0	0.0
Roseate Tern	Langham (1974)	-	-	99	5	5.0	0	0.0
Gannet	Nelson (1966)	500	55	445	35	7.9	0	0.0
Manx Shearwater	Harris (1966)	56	7	49	5	10.2	0	0.0
Audubons Shearwater	Harris (1969)	230	92	138	2	1.4	0	0.0
Razorbill	Plumb (1965)	86	27	59	0	0.0	0	0.0
Puffin	Nettleship (1972)	552	166	386	39	10.1	0	0.0
Puffin	Myrberget (1962)	48	1	47	1	2.1	0	0.0
All species				9 914	797	8.039	36	0.395

Furthermore, the frequency of abnormalities in chicks which hatch successfully is similar to that found in a number of populations contaminated by PCB and mercury, but much higher than in the few uncontaminated seabird populations which have been examined for abnormalities (table 97).

It seems probable that the high mortality at hatching and the high incidence of abnormalities are symptoms of PCB poisoning, and this might also be taken to explain the high numbers of addled eggs. However, of 122 "addled" eggs collected in 1976, 85 (70%) had no visible embryonic development and 37 (30%) had embryos at various stages of development. This meant that 12.5% of eggs were infertile and that 6.2% of all surviving fertile eggs suffered embryonic death. While PCBs increase embryonic death, they do not cause or increase infertility. Mercury can cause embryonic death, and can also disturb cell division (Ramel 1967), resulting in reduced fertility, but in view of the high mercury levels tolerated by Herring Gulls it seems improbable that it is reducing the fertility of Great Skuas.

Unfortunately, studies of nest histories very rarely differentiate between infertile eggs and eggs containing dead embryos, so it is not possible to estimate the normal frequency of these two categories separately.

Infertility may result from inbreeding of an isolated small population (Falconer 1960, Crow & Kimura 1970). The Great Skua in Britain appears to be genetically isolated from the Icelandic and Faroe populations, as no chicks have subsequently been found breeding in a country other than that in which they were ringed, no colour ringed individuals have been seen in a different country, even in the non-breeder club areas, and egg measurements differ between the three countries (table 98). Since 1700, the British Great Skua population

Table 97. Frequencies of gross abnormalities of successfully hatched chicks in seabird populations from polluted and unpolluted areas (taken from Hays & Risebrough 1972) and in Great Skuas on Foula.

Species	Locality	Pollutants	Deformed chicks	% deformed
Sooty Tern	Dry Tortugas	unpolluted	1 of 125000	0.0008 %
California Gull	Wyoming	unpolluted	4 of 6543	0.06 %
Common Tern	New York 1969	PCB, DDE, mercury	1 of 2089	0.04 %
Common Tern	New York 1970	PCB, DDE, mercury	35 of 2316	1.50 %
Roseate Tern	New York 1970	PCB, DDE, mercury	5 of 806	0.60 %
Great Skua	Foula 1975	PCB, mercury	6 of 1401	0.43 %
Great Skua	Foula 1976	PCB, mercury	11 of 2300	0.48 %
Great Skua	Foula 1977	PCB, mercury	3 of 1400	0.21 %

Table 98. Measurements of Great Skua eggs from Iceland, Faroe and Shetland colonies. Standard errors are given in parentheses. Four pairs of significant differences ($p < 0.05$) are marked with *.

Source	Area	category	sample size	length	breadth
BM (NH)	Iceland	all eggs	30	70.23 (0.48)	49.69 (0.25)
Potts (1961)	Iceland	all eggs	100	71.43	50.24
Potts (1961)	Faroes	c/1	21	73.40 *1 (0.66)	50.33 (0.37)
		c/2 (a)	178	73.12 *2 (0.22)	50.75 *3 (0.10)
		c/2 (b)	178	71.60 *4 (0.21)	50.18 (0.10)
Witherby et al (1941)	Britain	all eggs	100	70.58	49.06
This study	Foula	c/1	85	71.30 *1 (0.34)	49.81 (0.18)
		c/2 (a)	731	72.38 *2 (0.10)	50.02 *3 (0.04)
		c/2 (b)	731	70.11 *4 (0.09)	50.26 (0.04)

has experienced one "founder effect" and three genetic "bottlenecks" (brought about by human persecution and so probably non-selective), with intervening periods of population explosion (in which natural selection is reduced and much mortality is non-selective). This could have led to the recombination of deleterious genes and to excessive homozygosity through inbreeding, and could explain the high observed levels of infertility.

Great Skuas in the Faroes had a similar history of bottlenecks, persecution and population explosion, but Icelandic Great Skuas have not experienced any of these phenomena, remaining stable in numbers for many generations. As pollutant levels appear to be very similar in British and Icelandic Great Skuas, the relative effects of pollutants and inbreeding could be discerned by comparing nest histories of each Great Skua population. If inbreeding is occurring, it should be detected in Britain and in Faroe, but not in Iceland. Pollutant effects should be seen equally in all three countries.

Influence of age and experience on breeding

Pairs which established territories in the Ristie area in 1975 before 17 April tended to be experienced breeders (14 of 17 pairs which arrived before 17 April were experienced breeders compared to 5 of 15 pairs which arrived after 16 April; $X^2_1 = 7.95$, p 0.005), and pairs which returned early also laid earlier than pairs which arrived later (mean hatching date of pairs which arrived before 17 April (days after 31 May) was 19.41 (se = 1.44); mean hatching date of pairs which arrived after 16 April was 29.40 (se = 2.44), $t_{30} = 3.53$, p 0.01). This difference could be due either to the inexperience of late arriving pairs or to the better physiological condition of earlier arriving pairs.

Only five pairs were located in 1975 or 1976 which comprised two colour ringed individuals. Of these, mates in three pairs were of the same age and in two pairs the birds differed in age by one year. Studies of seabird species where larger numbers of breeding known-age birds are available show that members of pairs are usually of closely similar ages (cf. Coulson 1966). I have assumed this to hold true for the Great Skua. In 1976, a total of 38 of the 372 study territories contained a colour ringed individual. These birds were aged between five and eight years, and therefore unlikely to have bred for more than one or two previous seasons. Comparing the breeding success and hatching dates of these birds with pairs without colour rings, many of which will have bred together for more than three years, showed no significant difference in any of the measured parameters (table 99).

Table 99. Breeding statistics of colour ringed (relatively inexperienced) pairs and pairs without colour rings on Foula in 1976. Standard errors are given in parentheses.

Parameter	Colour ringed	Not colour ringed	Difference
sample size	38	334	
clutch size	1.92 (0.044)	1.93 (0.014)	ns
number hatched	1.45 (0.111)	1.45 (0.041)	ns
number fledged	1.44 (0.111)	1.38 (0.042)	ns
% addled eggs	21.1	16.8	ns
hatching date	17.40 (1.150)	17.37 (0.480)	ns
Aggression score	3.26 (0.105)	3.05 (0.053)	ns

Comparison of pairs of known breeding experience, but generally of unknown age, nesting in the Ristie area (table 100) shows no significant difference between birds breeding for the second, third, or at least third time, but birds breeding for the first time show significantly later hatching dates (and therefore laying dates), and show a significantly higher incidence of chick starvation ($X^2_1 = 17.5$, $p < 0.001$). This starvation resulted from a lack of parental attention when the chick(s) were very young, and appeared to be due to a failure of the parents to respond to the chicks rather than their inability to obtain food.

The clutch size of first-time breeders is often smaller than that of experienced pairs, but there is little evidence of this in Great Skuas. Similarly, the proportion of addled eggs shows no clear trend with experience, although Richdale (1954) found a greater incidence of addled eggs in inexperienced penguins.

Great Skua pairs in the Ristie area were studied in 1975 and 1976. Hatching dates of the same pair in successive seasons were significantly earlier in the second year of breeding than in the first ($\bar{d} = 8.63$ days, paired $t_7 = 4.02$, $p < 0.01$), earlier in the third than in the second ($\bar{d} = 4.67$ days) although the difference is not significant (paired $t_5 = 1.67$, ns) and no different between seasons for pairs which had bred at least twice before ($\bar{d} = -0.18$, $t_{10} = 0.08$, ns).

One reason for the lack of an experience related trend in the percentage of addled eggs may be the tendency of pairs to lay either addled or non-addled eggs in successive years. In the 1975 and 1976 seasons, 12 Ristie pairs laid non-addled clutches in both years, seven laid clutches with at least one addled egg in both seasons, but only six pairs laid non-addled eggs in one season and addled

Table 100. Breeding statistics of Great Skuas of known breeding experience. Standard errors are given in parentheses.

Parameter	Breeding experience (years previous breeding)			
	0	1	2	2+
sample size (pairs)	20	16	6	22
clutch size	1.80 (0.09)	1.94 (0.06)	1.83 (0.17)	1.91 (0.06)
number hatched	1.25 (0.19)	1.25 (0.19)	1.17 (0.40)	1.36 (0.15)
number fledged	0.90 (0.20)	1.19 (0.21)	1.17 (0.40)	1.32 (0.15)
hatching date	31.55 (1.71)	20.69 (1.41)	17.50 (1.86)	17.50 (1.28)
% addled eggs	28.6	33.3	36.4	18.4
number chicks starved	7/25	0/20	0/7	0/30

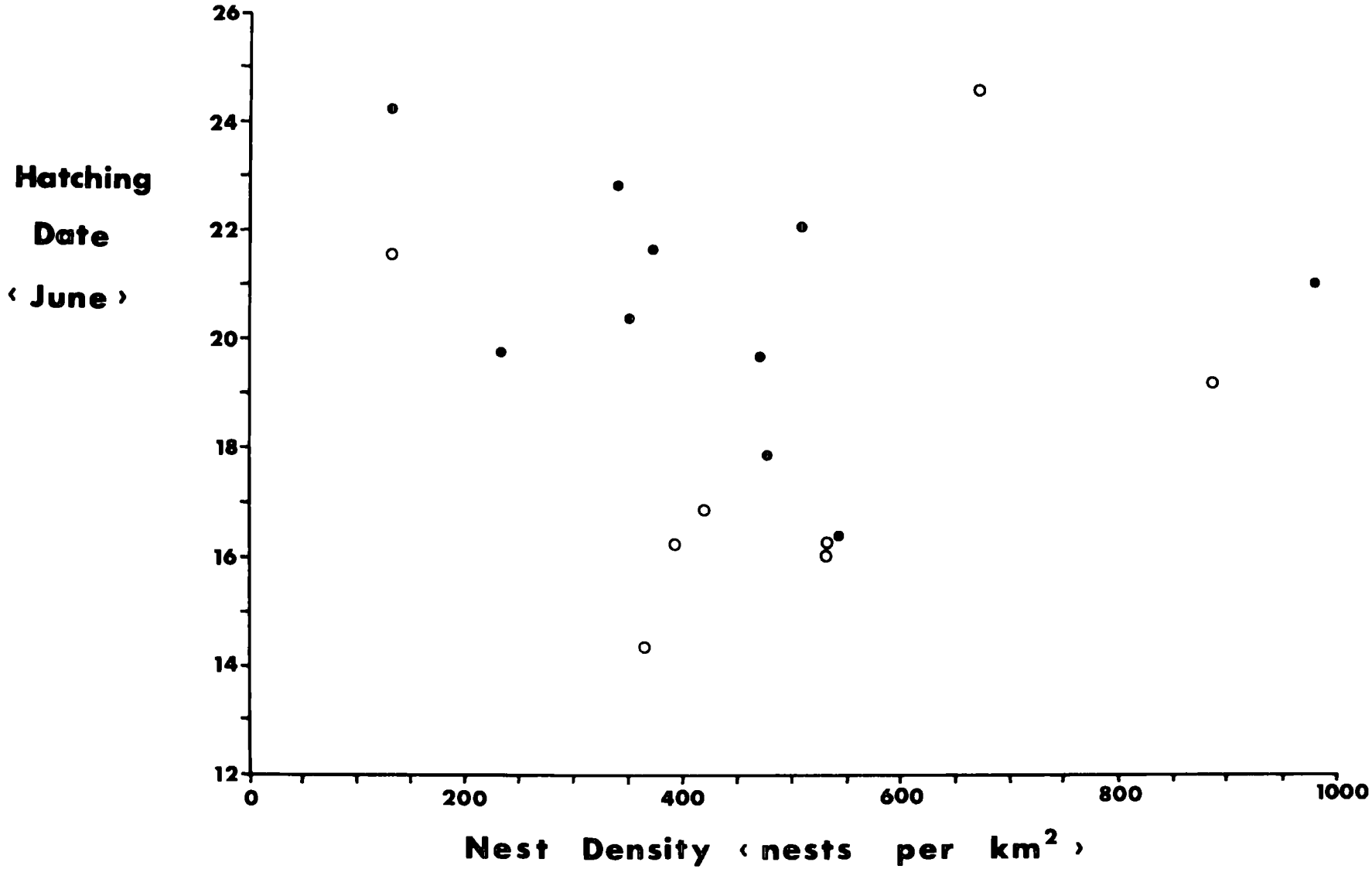
egg(s) in the other. The numbers differ significantly from random ($X^2_1 = 6.5$, $p < 0.025$), suggesting that the tendency might be genetic, or alternatively, that females obtain similar pollutant loads each winter, so that those with consistently high loads consistently produce addled eggs.

Influence of density on breeding

The kittiwake may be described as being adapted for colonial breeding because its breeding success is greater at higher nest densities, principally because laying is earlier (Coulson & White 1960, 1961, Coulson 1972). Similarly, the breeding success of Herring Gull pairs is greater if they nest early and synchronously, and this is effected through coloniality (Parsons 1971, 1975). Skuas may nest in isolation, at low density over wide areas, or in distinct colonies. To determine whether Great Skuas are adapted for colonial breeding or only breed in colonies when nesting space is limited, areas A and B were divided into sections of differing nest densities, and breeding statistics were calculated separately for each section.

Great Skuas showed no tendency to lay earlier at higher nest densities in 1975 ($r = -0.302$, $t_8 = 0.90$, ns) or in 1976 ($r = 0.175$, $t_6 = 0.44$, ns) (figure 36), while the mean number of chicks fledged per pair decreased with increasing nest density of subareas in 1975 ($r = -0.641$, $t_8 = 2.36$, $p < 0.05$) and in 1976 ($r = -0.212$, $t_6 = 0.53$, ns) although the trend is not significant in 1976. Breeding failure at high nest densities was not due to chick losses, as fledging success (% of chicks hatched which fledged) showed no trend with density in 1975 ($r = -0.082$, $t_8 = 0.23$, ns) or in 1976 ($r = 0.042$, $t_6 = 0.10$, ns). Clearly egg losses at high nest densities account

Figure 36. The relationship between the mean hatching date of each study subarea and nest density of that area. Hatching dates are measured in days after 31 May. Nest density is measured in nests km^{-2}. There is no significant trend with density either in 1975 (•) or in 1976 (o).


Hatching
Date
‹ June ›
26
24
22
20
18
16
14
12
0
200
400
600
800
1000
Nest Density ‹ nests per km² ›

for the observed trends. The proportion of eggs rolled out of nests, addled or dying at hatching did not vary with nest density, but the proportion of eggs taken by predators was highly correlated with nest density in 1975 ($r = 0.829$, $t_8 = 4.19$, $p < 0.01$) and showed a similar, but not significant, trend in 1976 ($r = 0.381$, $t_6 = 1.01$, ns). Egg predation (figure 37) appears to be the principal cause of the reduction in hatching success at high nest densities.

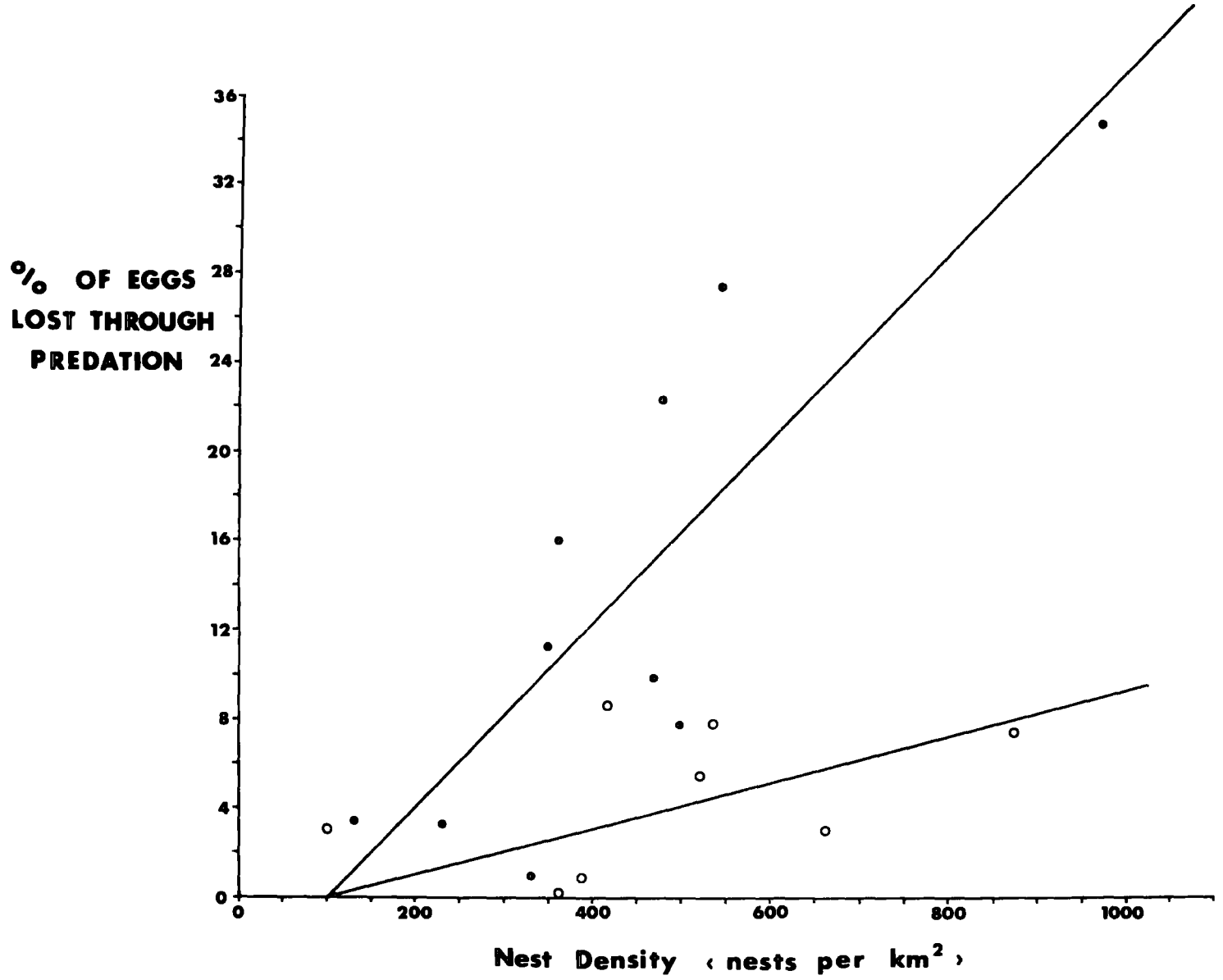
All this egg predation appeared to be effected by other Great Skuas. Nonbreeding Great Skuas are very rarely able to land in an occupied territory without being immediately chased away, and rarely attempt to do so, so it seems more likely that off duty neighbouring territory owners are the predators. Egg predation was considerably more likely to occur where the aggression score of the parents was low (table 101). In areas A and B pairs with the highest aggression index lost no eggs to neighbours, but pairs with the lowest index lost one or both eggs in between 36% and 100% of territories.

The mean aggression index of pairs did not show a significant trend with subarea density in either 1975 ($r = -0.289$, $t_8 = 0.85$, ns) or in 1976 ($r = -0.328$, $t_6 = 0.85$, ns) although in both years pairs in high density areas were slightly less aggressive. It is clear from table 101 that the differences in predation rate between areas were not due to differences in aggressiveness of pairs between areas, but as the level of predation increases due to increasing nest density, the chances of losing eggs to neighbours increases for all aggression categories. Thus density seems to modify the level of egg predation, and the aggressiveness of each pair determines the chance of their losing eggs. The much greater egg predation in 1975 than in 1976 parallels food availability, which was greater in the second year (section 4). When not foraging, off duty birds spend

Table 101. Numbers of pairs in each aggression category which lost one or both eggs to predation by neighbours in area A in 1975 and area B in 1975 and 1976.

Area and year	Category	Aggression score 1	2	3	4	5	Totals
A 1975	Predated clutches	11	27	13	4	0	55
	Total laid	11	43	53	63	14	184
	Percentage taken	100	63	24	6	0	30
B 1975	Predated clutches	6	13	4	1	0	24
	Total laid	11	58	96	73	23	261
	Percentage taken	54	22	4	1	0	9
B 1976	Predated clutches	9	10	4	0	0	23
	Total laid	25	59	172	98	18	372
	Percentage taken	36	17	2	0	0	6

Figure 37. The relationship between nest density and the percentage of Great Skua eggs lost through predation by conspecifics in subareas of Foula in 1975 (•) and 1976 (o).


% OF EGGS LOST THROUGH PREDATION
36
32
28
24
20
16
12
8
4
0
0
200
400
600
800
1000
Nest Density ‹ nests per km² ›

virtually all the spare time on their territory, and it is they who repel intruding birds, while their mate incubates. If food is scarce the mate is left alone for longer periods, and off duty neighbours would have a chance to steal an egg, whereas they would have little chance if two birds were present. It could be predicted that egg predation would be temporally clumped, occurring particularly during periods of low food availability. Predation dates are strongly clumped for area in 1975, and slightly clumped for area B in 1975, but almost randomly distributed for area B in 1976 (table 102). Thus the area of highest nest density and highest rate of egg predation showed the greatest temporal heterogeneity (figure 38).

There was no clear correlation between numbers of clutches lost on each date in areas A and B in 1975 ($r = 0.145$, $t_{38} = 0.90$, ns), suggesting that temporal variation in food availability does not cause day to day variations in egg predation rates. I obtained an impression in the field that the loss of a clutch was particularly likely to lead to the loss of clutches of closely neighbouring pairs. Unfortunately the statistical analysis of space-time interaction (Besag & Diggle 1977) is not yet sufficiently well developed to test this observation simply. I think it is probable that food shortage increases the chances that off duty birds may steal the eggs of a neighbouring pair while only one bird is present on the territory, and once their eggs have been taken the pair is likely to steal eggs from one of their neighbours, particularly when neighbours are nesting close by (i.e. nest density is high). This leads to temporally and spatially synchronous egg predation which, particularly affects pairs with low aggression indices and is more frequent in seasons of low food availability and in areas of high nest density.

Why then do some pairs nest at much higher densities than others?

Figure 38. Numbers of clutches lost each day as a result of egg predation in area A in 1975 (A), area B in 1975 (B) and area B in 1976 (C).

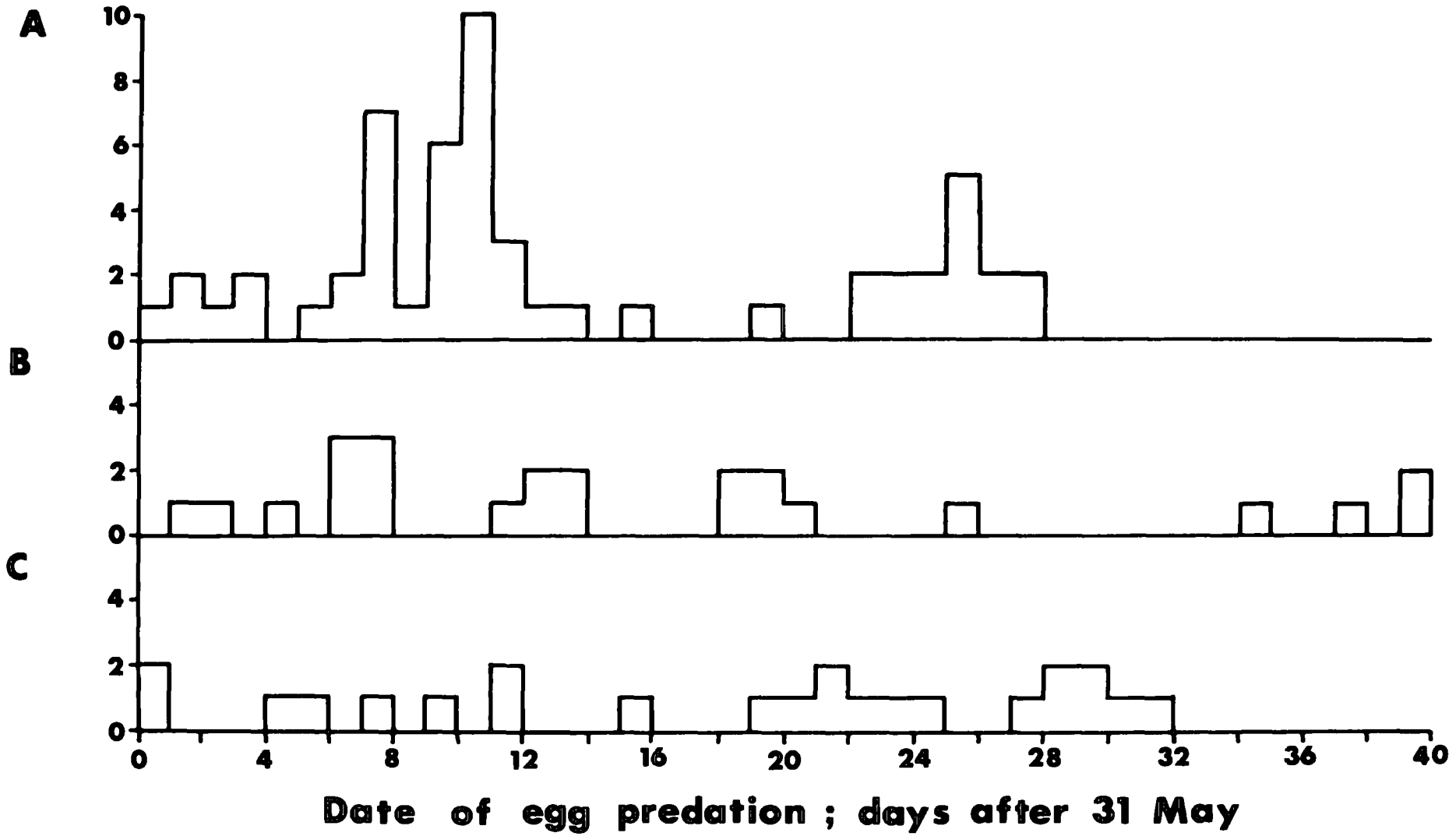

A
B
C
10
8
6
4
2
0
4
2
0
4
2
0
0
4
8
12
16
20
24
28
32
36
40
Date of egg predation ; days after 31 May

Table 102. Numbers of clutches stolen in two day intervals from 31 May in area A in 1975 and area B in 1975 and 1976.

Number of clutches taken	area A 1975 number of times	area B 1975 number of times	area B 1976 number of times
0	8	8	7
1	3	8	6
2	1	1	5
3	2	0	1
4	2	2	1
7	2	0	0
9	1	0	0
13	1	0	0
Total taken (clutches)	55	24	23
Number of time intervals	20	20	20
Mean number taken per time interval	2.75	1.20	1.15
Variance	13.36	2.70	1.29
Coefficient of dispersion	4.86	2.25	1.12

One striking feature of large Great Skua colonies is the presence of "club" areas used by prebreeders. These are surrounded by a large number of very small breeding territories ("club territories"). Pairs in these territories tend to have low aggression scores and late hatching dates (table 103).

These pairs seem to be poor quality individuals, unable to obtain non-club territories and forced to nest around club sites (equivalent to the "edge" pairs of nesting Kittiwakes (Coulson 1968)). There is no indication that they are mainly first time breeders, as none of the 86 birds in club areas in 1976 had colour rings. Nest density in these club areas is ten times higher than in most colony areas, reaching 4000 pairs km^{-2} around one club site. The low aggressiveness of pairs in club territories may allow such high nest densities (figure 39).

In both club areas and in area B territories nest densities and mean hatching dates differed considerably between the 1975 and 1976 breeding seasons (figure 40). In 1976 laying dates were earlier and nest densities higher than in 1975. If food was more abundant in 1976 early in the season, as it was later, this may have allowed both earlier breeding and larger numbers of recruits into the breeding population.

Fledging success of club pairs is lower than of non-club pairs. This is largely due to lower hatching success, which is due to higher egg predation in club areas. As with subareas of differing densities, egg predation in club areas was much greater in 1975 than in 1976; only in 1975 was there a significant trend with nest density (figure 41).

In colonies where nesting space is less restricted, poor quality individuals may establish territories on the colony edge. These

Table 103. Breeding statistics of pairs in club territories and non-club territories in area B on Foula in 1975 and 1976

Parameter	non-club pairs 1975	non-club pairs 1976	club 1 1975	club 1 1976	club 2 1975	club 2 1976
sample size (pairs)	229	329	26	27	6	16
area (km^2)	0.730	0.713	0.015	0.012	0.002	0.004
pairs / km^2	314	462	1711	2328	2727	4000
Chicks fledged per pair	1.271	1.432	1.038	1.222	0.667	0.687
standard error	0.051	0.040	0.130	0.154	0.333	0.198
Aggression index mean	3.266	3.155	2.269	2.815	2.500	1.687
standard error	0.064	0.048	0.152	0.220	0.428	0.218
Mean hatching date						
days after 31 May	20.65	16.43	25.04	20.11	33.83	32.25
standard error	0.50	0.43	1.93	1.85	2.77	2.12

Figure 39. Mean aggression scores of pairs in non-club territories and in territories around two club sites in area B of Foula in 1975 (★) and 1976 (☆). 95% confidence limits for each mean aggression score (± 2 se) are marked. Mean scores are plotted against mean nest densities for each category, showing a tendency for club pairs to have low aggression scores and to nest at high densities.

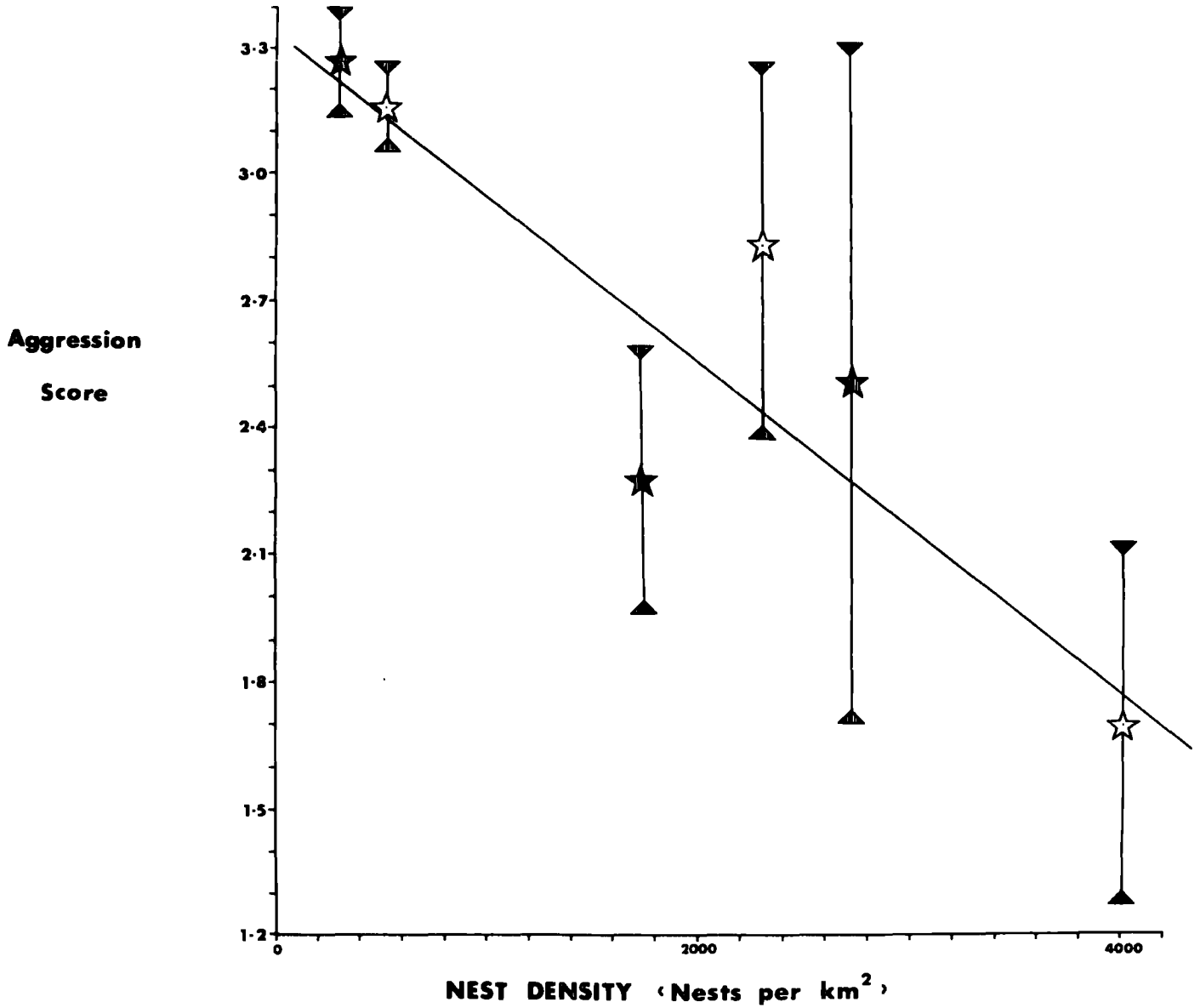

Aggression
Score
3·3
3·0
2·7
2·4
2·1
1·8
1·5
1·2
0
2000
4000
NEST DENSITY (Nests per km²)

Figure 40. Mean hatching dates of pairs in non-club territories and in territories around two club sites in area B of Foula in 1975 (●) and in 1976 (☆). 95% confidence intervals for each mean hatching date (± 2 se) are marked by bars. Mean dates are plotted against mean nest densities for each category.

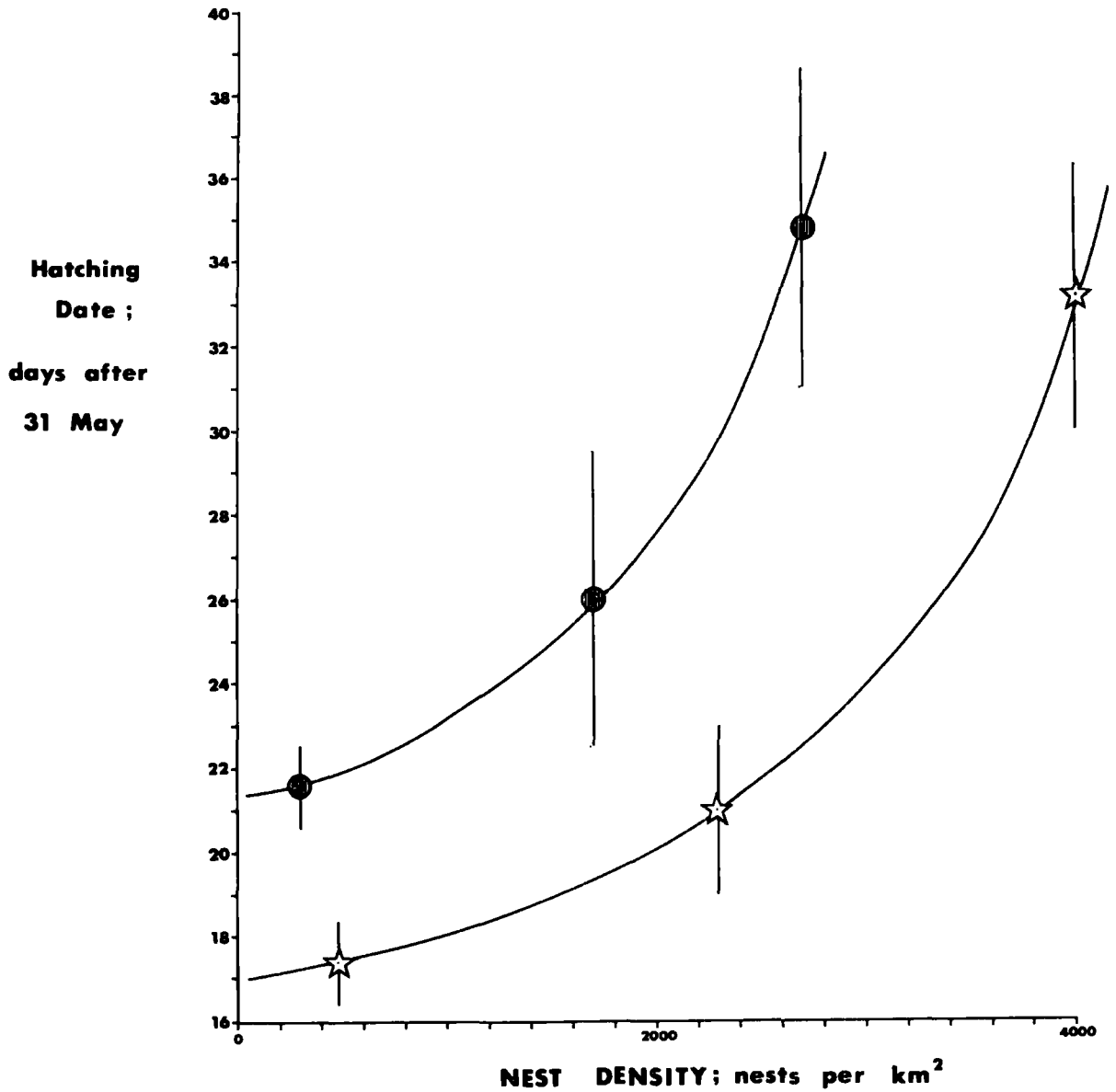
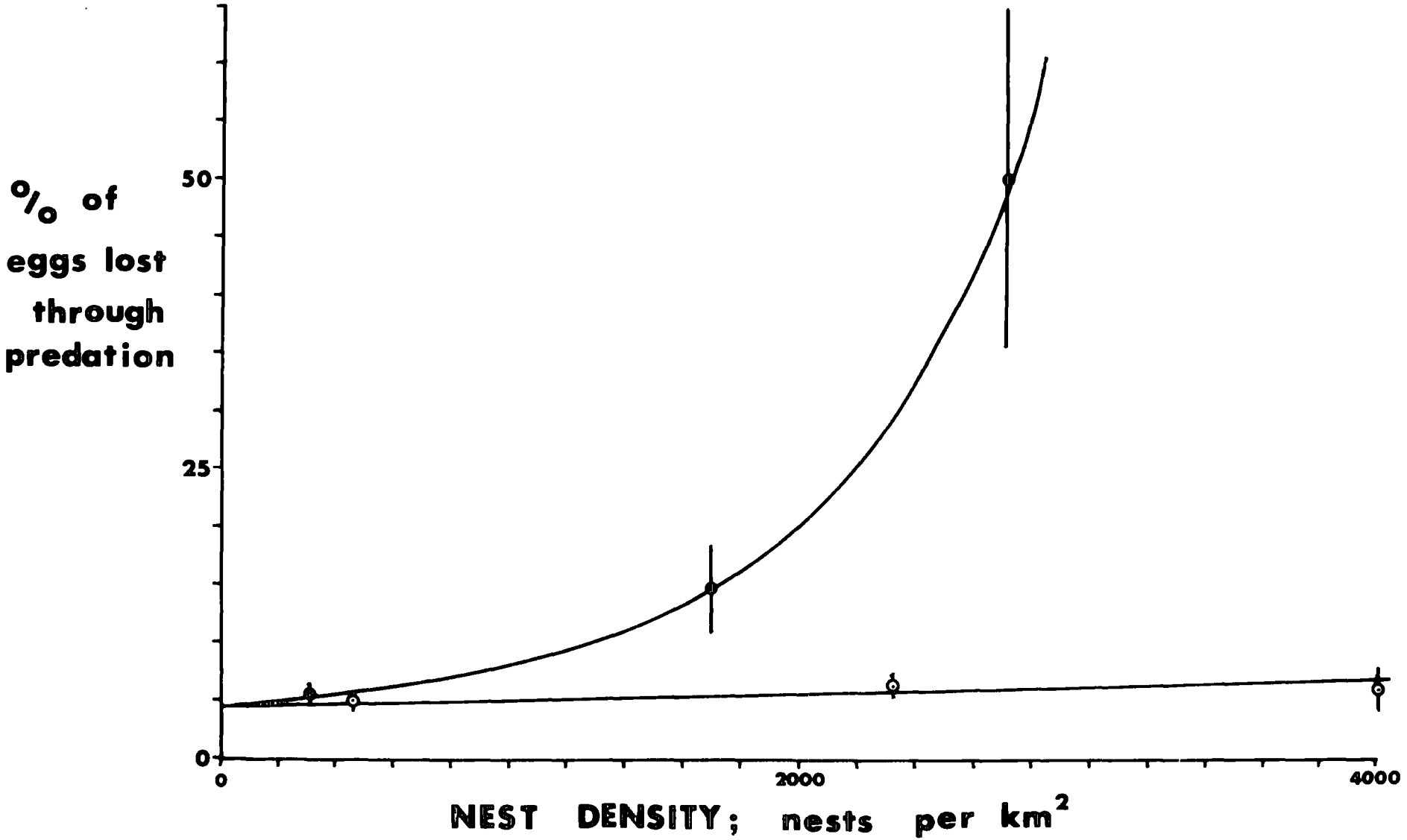

Hatching
Date ;
days after
31 May
40
38
36
34
32
30
28
26
24
22
20
18
16
0
2000
4000
NEST DENSITY; nests per km²

Figure 41. The relationship between nest density of non-club and club territories and the percentage of eggs lost through predation in 1975 (●) and 1976 (o). (95% confidence intervals for means ($\pm$ 2 se) are marked by bars).


% of eggs lost through predation
50
25
0
0
2000
4000
NEST DENSITY; nests per km²

territories tend to be larger than average. The presence of poor quality pairs in large edge territories and in small club territories gives a maximum breeding success at an intermediate nest density, as can be shown from a reanalysis of data collected by Perry (1948) from Noss in 1946 (figure 42). This curve is a function of pair quality, and may not be influenced by nest density per se, as nest density on Noss in 1946 was very much lower than that on Foula in this study. At present on Foula, few vacant edge areas remain for Great Skuas to spread onto, and recruitment is almost entirely into established non-club territories or into poor quality club territories.

Clearly nesting density on Foula is higher than the optimum for this species, and as a result, hatching success is reduced, particularly in poorer quality pairs and in seasons of low food availability.

Relative rates of egg and chick mortality factors

Using all nest histories from areas B and C in both 1975 and 1976, and area A in 1975, rates of egg and chick mortality factors were compared between first and second laid eggs in clutches of two, then between clutches of two and clutches of one egg.

Only the proportion of chicks which starved to death differs significantly between first and second laid eggs (table 104). Second hatched chicks were three times as likely to starve as first hatched, this difference being due to the asynchronous hatching which enables the older chick to dominate its sibling when competing for food from the parents.

Clutches of one egg showed significantly higher rates of mortality due to egg predation, addled eggs and chick starvation (table 105). Pairs laying single eggs had significantly lower aggression scores than pairs laying two eggs ($t_{878} = 2.96$, $p < 0.01$), so it

Figure 42. Mean numbers of chicks fledged per pair in relation to the mean distance to the nearest neighbour for subareas of the Great Skua colony on Noss. These data were taken from Perry (1948).

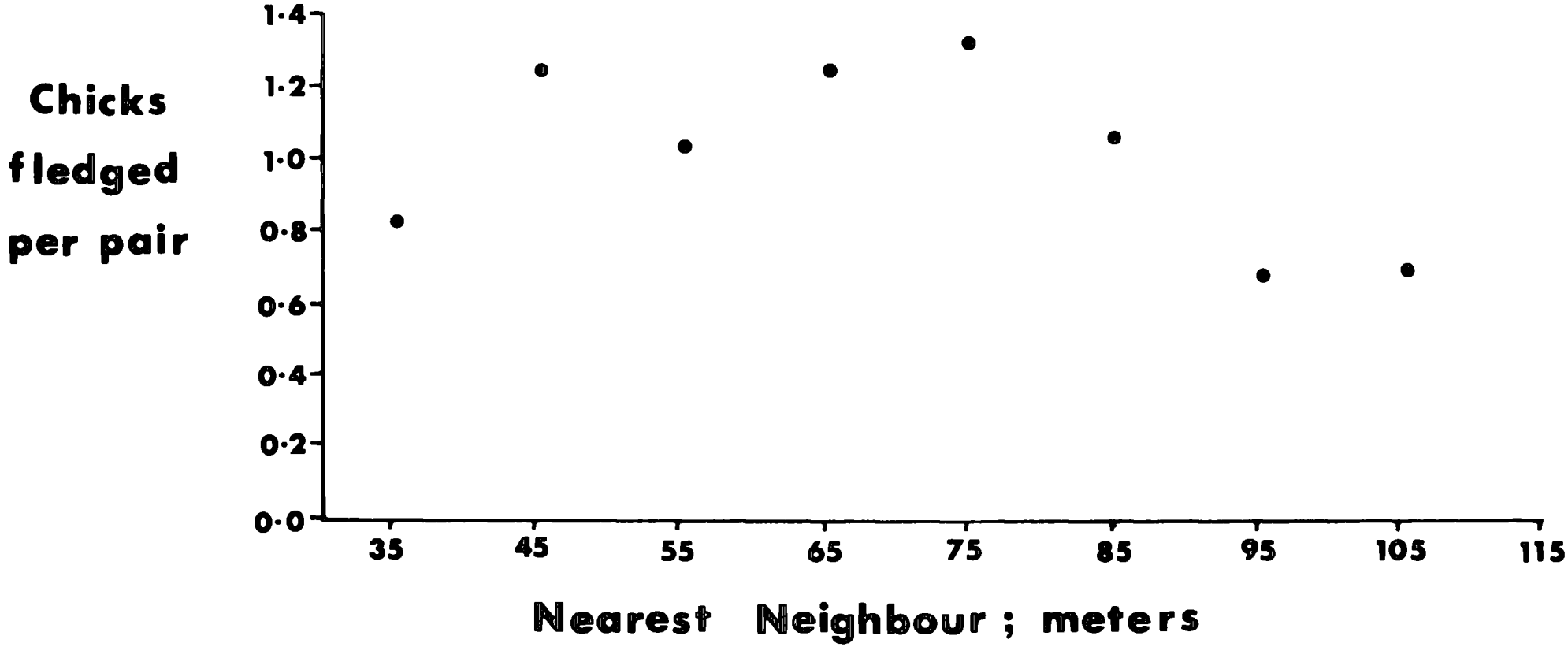

Chicks fledged per pair
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0·0
35
45
55
65
75
85
95
105
115
Nearest Neighbour ; meters

Table 104. Differences in the rates of egg and chick mortality factors between first and second laid eggs in Great Skua clutches of two eggs. Expected values are given in parentheses.

Mortality factor	first laid	second laid	χ^2_1	significance
Predation	79 lost of 787 (78.0)	77 lost of 787 (78.0)	0.028	ns
Rolled out of nest	24 lost of 787 (19.5)	15 lost of 787 (19.5)	2.128	ns
Addled	107 lost of 684 (110.1)	115 lost of 695 (111.9)	0.206	ns
Died hatching	14 lost of 577 (17.0)	20 lost of 580 (17.0)	1.062	ns
Starved to death	7 lost of 563 (14.5)	22 lost of 560 (14.5)	7.964	$p < 0.005$
Chick predated	16 lost of 563 (18.5)	21 lost of 560 (18.5)	0.699	ns
Mutant	3 lost of 563 (3.0)	3 lost of 560 (3.0)	0.000	ns

Table 105. Differences in the rates of egg and chick mortality factors between clutches of one and of two eggs laid by Great Skuas in Foula study areas. Expected values are given in parentheses.

Mortality factor	clutches of one	clutches of two	X_1^2	significance
Predation	21 lost of 93 (9.9)	156 lost of 1574 (167.1)	14.76	$p < 0.005$
Rolled out of nest	2 lost of 93 (2.3)	39 lost of 1574 (38.7)	0.04	ns
Addled	27 lost of 70 (12.0)	222 lost of 1379 (237.0)	23.78	$p < 0.005$
Died hatching	0 lost of 43 (1.2)	34 lost of 1157 (32.8)	1.27	ns
Starved to death	6 lost of 43 (1.3)	29 lost of 1123 (33.7)	18.20	$p < 0.005$
Chick predated	0 lost of 43 (1.4)	37 lost of 1123 (35.6)	1.45	ns
Mutant	0 lost of 43 (0.2)	6 lost of 1123 (5.8)	0.23	ns

appears that single egg clutches tend to be laid by poor quality pairs; it was shown earlier that there was no tendency for inexperienced or young pairs to lay smaller clutches than experienced or older pairs. The higher proportion of addled eggs in single egg clutches again points to poor quality parents, and suggests that parent quality may have a genetic component, possibly being related to the degree of inbreeding of the individual. The high rate of starvation of chicks hatched from single egg clutches cannot be due to food shortage per se, as starvation is less frequent even in chicks from second laid eggs in clutches of two. Either some pairs laying single eggs are of such poor quality that they are not even capable of obtaining sufficient food to raise even one chick, which seems unlikely, or they are not sufficiently motivated to do so.

As 90% of pairs in the study areas laid clutches of two eggs, the fate of these largely determines overall mortality rates. The study nests are taken to be representative of all areas of the island, covering the extremes of nest density found in this colony, but were examined only in two seasons of apparently above average food availability, so probably represent above average breeding success for Foula. Addled eggs were the cause of the greatest reduction in breeding success, followed by egg predation (table 106). These two factors accounted for 74% of all egg and chick losses.

In view of the ability of gulls to roll eggs back into the nest (Tinbergen 1953), it is surprising that Great Skuas show no tendency to do so, particularly as 2.5 % of all eggs in study nests were lost through being rolled out of the nest. There was no tendency for these to be addled eggs, so they were not likely to have been deliberately ejected.

Table 106. Rates of egg and chick mortality in all study nests of Great Skuas on Foula in 1975 and 1976.

Parameter	number	mortality (%)	parameter as % of:
Eggs laid	(1667)		100%
Eggs predated	177	10.6	% of all eggs laid
Eggs rolled out of nest	41	2.5	% of all eggs laid
Eggs addled	249	17.2	% of those eggs fully incubated
Eggs with embryo at hatching	(1200)		
Eggs died at hatching	34	2.8	% of those eggs with embryos
Hatched	(1166)		69.9 % of all eggs laid
Chicks starved	35	3.0	% of those hatched
Chicks predated	37	3.2	% of those hatched
Mutant chicks (grossly abnormal)	6	0.5	% of those hatched
Fledged	(1088)		93.3 % of those hatched
Fledged	(1088)		65.3 % of all eggs laid

SECTION 6

INTERACTIONS WITH THE ARCTIC SKUA DURING THE BREEDING SEASON

Literature

Many authors (e.g. Pennie 1948, Baxter & Rintoul 1953, Venables & Venables 1955) have claimed that the 20th century increase of the Great Skua has resulted in a decrease in numbers of Arctic Skuas breeding in Shetland colonies, but their views have been supported only by circumstantial evidence. Pennie (1948), after visiting Foula, stated that Arctic Skua numbers were "diminishing owing to the ravages of the Bonxies; practically none of the young being allowed to reach maturity", but he provided only one estimate of the number of birds in the Arctic Skua population of the island. Jackson (1966) recorded that Great Skuas kill Arctic Skua chicks, and, because they return to the colony earlier in the year, they may establish territories in areas formerly occupied by Arctic Skuas, which, when they return to the island, are unable to regain their territory from the larger and more powerful species. He considered that inter-specific territoriality, coupled with the general increase of Great Skua numbers and the similarity of the nesting requirements of the two species, would have a more serious long-term influence on Arctic Skua populations than direct predation by Great Skuas. Because the two species are closely related, being either congeneric or in adjacent genera, interspecific competition might be expected in the feeding of the two species. These three interactions seem likely to have adverse effects on the two species, particularly on Arctic Skuas, but have not previously been quantitatively studied. Nor has any

attempt been made to collect and interpret the estimates of Shetland Arctic Skua colony sizes recorded by numerous ornithologists since 1890. The Arctic Skua is one of the least numerous of our breeding seabirds; about 70% of the British population breeds in Shetland (Cramp et al. 1974, Everett 1977), so that conservation of this species would depend largely on the maintenance of its breeding colonies in Shetland. The largest British Great Skua colonies are adjacent to large Arctic Skua colonies, on Foula, Unst and Noss, so it is in these areas that interspecific interactions would be expected. Published and unpublished census data for these three colonies, and quantitative observations of interspecific interactions are examined in this section, to determine whether either species is noticeably affected by the other.

Census data for Arctic Skua colonies

Problems of censusing Great Skuas (section 1) also apply to Arctic Skuas. Most censuses have been of pairs occupying territories, or were made by mapping the position of all territories onto a map of the colony. A very few were made by marking all nests found. These different methods give reasonably consistent results when used independently in the same colony (table 107); problems associated with censusing large colonies do not arise, as no British Arctic Skua colony contains more than 320 breeding pairs, and most contain fewer than 100.

In other parts of Britain where there are few Great Skuas, Arctic Skua numbers have probably changed little, but with suggestions of decreases in Northern Scotland and increases in Orkney (Cramp et al. 1974); census data for Shetland should be examined against this

Table 107. Estimates of pairs of Arctic Skuas on Foula, obtained by different census methods.

Year	Source of estimate	Method used	Estimate (pairs)	Difference between methods (%)
1965	Fabritius (1969)	mapping pairs	140	15 %
	Brathay	count of pairs	120	
1974	Davis (in litt.)	count of pairs	200	10 %
	this study	mapping pairs	180	
1975	Davis (in litt.)	marking nests	253	5 %
	this study	mapping pairs	240	

background. Numbers on Noss have fluctuated considerably, from 13 to 60 pairs, but show no long term trend, the number of pairs now being the same as that recorded in 1922 (table 108). Data from Unst are less reliable: there has been a considerable decrease at Hermaness, but an increase in other parts of Unst; the total number of pairs over the whole of Unst appears not to have decreased by more than 10% since 1922 (table 109). These two Arctic Skua colonies have maintained themselves despite increases in the Great Skua populations, from a score of pairs on Unst and none on Noss in 1900 to the current totals of 1000 pairs on Unst and 250 pairs on Noss. The most thoroughly documented of the three colonies is that on Foula, where the Arctic Skuas have increased slowly and with some fluctuations, from 60 pairs in 1890 to 130 pairs in 1973, then suddenly to 190 pairs in 1974, 250 pairs in 1975 and 306 pairs in 1976 (table 110). This increase is all the more surprising when it is remembered that the Foula Great Skua colony is the biggest and densest in Britain. Clearly, any deleterious effects of either species on the other have been insufficient to cause population declines, and Arctic Skua numbers have even increased.

Great Skua predation on Arctic Skuas

Jackson (1966) recorded that, between 1956 and 1965, variable numbers of Arctic Skua fledglings were killed by Great Skuas. In 1960, it was estimated that 20% of fledglings were killed, whereas in 1961 only 2 to 5% were killed. Since 1969, all remains of kills attributed to Great Skuas on Foula have been recorded (Furness 1974c, 1976). From these records, the total number of Arctic Skua adults and fledglings killed each year can be expressed as a percentage of the number present on Foula (table 111). To determine the percentage

Table 108. Estimates of the number of pairs of Arctic Skuas on Noss.

Year	Source	Method	Estimate (pairs)
1922	Baxter & Rintoul (1953)	count of pairs	45
1929	Perry (1948)	count of pairs	60
1934	Perry (1948)	count of pairs	50
1939	Perry (1948)	count of pairs	25
1946	Perry (1948)	marking nests	31
1947	Baxter & Rintoul (1953)	count of pairs	37
1955	Kinnear (1974)	count of pairs	25
1957	Gordon (1964a)	count of pairs	13
1958	Kinnear (1974)	count of pairs	25
1964	Gordon (1964a)	count of pairs	17
1969	Kinnear (1974)	count of pairs	40
1970	Kinnear (1974)	count of pairs	40
1973	Kinnear (1974)	mapping pairs	39
1974	Kinnear (1974)	marking nests	44

Table 109. Estimates of the number of pairs, and nesting density (pairs/km^2) of Arctic Skuas at Hermaness, and on the rest of Unst.

Year	Source	Method	Hermaness		Rest of Unst	
			pairs	density	pairs	density
1922	Pitt (1922)	mapping pairs	200	29	0	-
1937	Baxter & Rintoul (1953)	count of pairs	100	-	-	-
1950	Gordon (1964b)	marking nests	75	17	-	-
1958	Gordon (1964b)	count of pairs	70	-	-	-
1965	Dott (1967)	mapping pairs	60	-	-	-
1969	Bourne & Dixon (1974)	count of pairs	80	-	-	-
1974	Bundy (1974)	mapping pairs	72	72	121	24

Table 110. Estimates of the number of pairs, and nesting density (pairs/km^2) of Arctic Skuas on Foula

Year	Source	Method	Estimate (pairs)	Colony area (km^2)	Density of pairs per km^2.
1890	Barrington (1890)	count of pairs	60	-	-
1948	Pennie (1948)	count of pairs	100	3.0	33
1960	Brathay	mapping pairs	131	2.3	57
1961	Brathay	count of pairs	130	-	-
1962	Brathay	count of pairs	120	-	-
1963	Brathay	count of pairs	120	-	-
1964	Brathay	count of pairs	120	-	-
1965	Fabritius (1969)	mapping pairs	140	-	-
1965	Brathay	count of pairs	120	-	-
1966	Brathay	count of pairs	120	-	-
1968	Brathay	mapping pairs	160	2.3	70
1969	Brathay	count of pairs	100	-	-
1972	Brathay	mapping pairs	150	2.0	75
1973	this study	mapping pairs	130	2.0	65
1974	this study	mapping pairs	180	1.8	100
1974	Davis (in litt.)	count of pairs	200	-	-
1975	this study	mapping pairs	240	1.8	133
1975	davis (in litt.)	marking nests	253	-	-
1976	this study	mapping pairs	306	1.4	218

Table 111. Predation of Arctic Skuas by Great Skuas on Foula.

Year	Pairs of Arctic Skuas	Numbers killed by Great Skuas:			
		Adults		Fledglings	
		number	%	number	%
1969	100	20	10.0	51	42.5
1970	120	3	1.2	14	9.7
1971	140	11	3.9	72	42.9
1972	150	19	6.3	56	31.1
1973	130	3	1.2	43	27.6
1974	190	21	5.5	35	15.4
1975	250	17	3.4	26	14.9
1976	300	7	1.2	36	10.0

of fledglings killed, an estimate of fledgling production per pair is required. Within the Foula colony, under conditions free from human disturbance, this is taken to be 1.2 chicks per pair, a value intermediate between those determined on Fair Isle, where nest density is lower (O'Donald 1962), and on Noss, where nest density is higher (Kinnear 1974).

The considerable variation in predation intensity appears to result from differences in the availability of fish during the weeks when Arctic Skua chicks begin to fly in different years. Killing of Arctic Skua adults occurs earlier in the summer than killing of fledglings, and adults are often not eaten, suggesting that adult mortality results from territorial disputes rather than predation for food. This supposition is supported by the low correlation between the numbers of adult and of fledgling Arctic Skuas killed in each of the eight years ($r = +0.282$, $p > 0.4$, ns.). In the long term, it is the mean predation rate which is most meaningful. The 3.7% predation of adults represents a 20% addition to the normal annual adult mortality, while the 21% loss of fledglings is nearly as great as the normal mortality in the whole of the first year of life. These values would be expected to result in a rapid decrease of Arctic Skua numbers on Foula if the population was closed and breeding effort at the species' physiological maximum. Neither of these conditions is likely, so detailed knowledge of the population dynamics of the species is required before these figures can be put in perspective. It is clear, however, that the proportion of Arctic Skua fledglings killed each year has increased since the observations by Jackson (1966), while the regular killing of Arctic Skua adults may be a new effect of the Great Skua as it has moved into traditional Arctic Skua areas, since it was not mentioned by previous authors.

Predation by Great Skuas on Arctic Skuas has been noted in the other main breeding areas (Lockie 1952, Kinnear 1974, Albon et al. 1976) but no quantitative data have been given by these authors. For the Great Skua, the importance of predation on Arctic Skua fledglings as a source of food can be easily assessed. An Arctic Skua fledgling weighs between 390 and 440 grams, averaging 410 g. Of this, about 100 g. will be inedible, so a Great Skua would obtain about 300 g. of food from each kill. Assuming a calorific value of 1.6 kcals g^{-1} of chick tissue (section 4) this weight is equivalent to 480 kcals. As an average of 42 Arctic Skua fledglings were killed in each year (table 111) the total energy taken is 42 x 480, or 2 x 10^4 kcals yr^{-1}. The total energy requirement of the Great Skua breeding population and chicks (not including nonbreeders as they are not responsible for the killing) during July, the month in which the killing occurs, is 7.36 x 10^7 kcals. Thus, Arctic Skua fledglings represent only 0.027% of the energy intake over this period. This is of negligible importance to the population as a whole, but may be a valuable supplement for opportunistic females in territories adjacent to areas of the Arctic Skua colony, as one kill would save the mate from spending many hours at sea obtaining the same food value of fish.

Interspecific competition for food

Arctic Skuas have never been recorded in feeding flocks of seabirds over surface fish shoals. It would be surprising if they were able to compete with the large species found in these flocks, as considerable fighting and jostling occurs, which would be likely to seriously injure a small species such as the Arctic Skua. Great Skuas are an important component of these flocks (section 4). I

have never seen Arctic Skuas fishing for themselves. Belopolskii (1961) records that of 63 observations of this species feeding in the open Barents Sea, 14 (22%) were of birds catching a fish for themselves, while the rest were seen robbing Kittiwakes (78%). Belopolskii does not state whether these were breeding birds or birds seen out of the breeding season, but as they were seen well out to sea, the latter seems more likely. Crowberries, insects, birds eggs and small birds up to the size of a Golden Plover, are eaten by breeding Arctic Skuas (Belopolskii 1961, personal observation), but these do not form an important proportion of the diet. As with the Great Skua, about 90 - 95% of food taken is fish, consisting almost exclusively of sandeels. Arctic Skuas in Shetland appear to obtain these sandeels entirely by kleptoparasitism. Thus, competition with Great Skuas for food would only arise if the two species conflicted in their kleptoparasitic activities. For the Great Skua, kleptoparasitism is only a minor feeding technique (section 4), so competition would be more likely to adversely affect the Arctic Skua, for which it is the principal feeding method.

Comparison of kleptoparasitic behaviour of Great and Arctic Skuas

At Foula, kleptoparasitism provides at least 90% of the energy intake of Arctic Skuas, but less than 10% that of Great Skuas (section 4). The median duration of foraging trips recorded during 24 hour hide watches of breeding pairs (35 minutes for Great Skua (section 4) and 38 minutes for Arctic Skua (this section)) indicates that these species feed mainly within a few kilometers of the island. If the skuas flew at 45 km hr^{-1}, and took no time to obtain their food, departure of 36 minutes would allow a skua to travel 14 km from its

territory. However, skuas do not fly directly when engaged in kleptoparasitism, but soar and glide, taking advantage of updrafts, particularly at cliff faces (pers. obs., Grant 1971). Victims are usually chased towards the breeding cliff, but many chases are required to provide a complete load of fish, so even individuals spending longer periods away from the territory probably do not travel more than a few kilometers from the island. Observations from Foula indicate that most chases are initiated within 1 km of the island, and as returning potential victims will be most dense near to the colony, it would seem a sensible strategy for skuas to intercept victims in this area. I saw very few skuas "patrolling" (Grant 1971) more than 2 km from Foula, although Great Skuas regularly travel at least 10 km to join feeding flocks over fish shoals. Thus observations from Foula clifftops of chases by skuas were thought to be representative of kleptoparasitic feeding activity of both species at this colony.

The ethology of kleptoparasitism has been discussed by Grant (1971), who studied interactions between Arctic Skuas and Puffins at an inland site in Iceland, by Furness (1973) who studied both skuas chasing a range of seabirds on Foula, and by Andersson (1976), who studied Great Skua chases of Gannets and Puffins and Arctic Skua chases of Puffins. All of these studies succeeded in finding relationships between the success of chases and other recorded parameters, but in no case was a sufficient number of observations collected to analyse causes of success or costs and benefits of chases by each skua species on each victim. To attempt this, two sites on Foula were chosen for watches. One was East Hoevdi, a good vantage point 75 m above sea level near large numbers of breeding Puffins, Guillemots, Razorbills, Fulmars and Kittiwakes, and near a regular

flight line of Gannets. The second was North Hoevdi, 40 m above sea level, beside the large Arctic Tern colony, and breeding colonies of Razorbills, Puffins and Kittiwakes. East Hoevdi was an area mainly of Great Skua activity while North Hoevdi was chiefly attended by Arctic Skuas, the difference reflecting both the breeding distributions of the two skuas on Foula and the numbers of their preferred victims at each site. Watches were maintained at intervals through the 1975 and 1976 breeding seasons. At each watch, the following details were recorded; site, date, time watch began, duration of watch in hours, local visibility (1-5; 1 = excellent, 5 = bad) and all chases by Great Skuas and by Arctic Skuas which were seen. For each chase the following were noted (table 112).

Table 112. Parameters recorded for each chase seen during watches of kleptoparasitism at Foula in 1975 and 1976.

Parameter	Parameter values
Species of skua	1 = Great Skua, 2 = Arctic Skua
Number skuas chasing victim	1 - 4
Species being chased	1 - 9: Arctic Tern, Kittiwake, Puffin, Razorbill, Guillemot, Gannet, Arctic Skua, Great B.-b. Gull, Herring Gull.
Height of victim above sea	25, 50, 100, 200 feet
Duration of chase	5, 10, 15, ... 50 seconds.
Speed of reaction to skua	1 - 3: 1 = fast, 2 = average, 3 = slow
Method of evasion	1 = outfly, 2 = dive into sea.
Result for victim	1 = fish retained, 2 = fish released
Number fish obtained by skua(s)	1 - 4 (always sandeels).

Meteorological data were obtained from Lerwick Observatory daily records and used in the analysis. Parameters taken were those listed in table 113.

Table 113. Parameters extracted from Lerwick Observatory files and added to data for each watch period.

Parameters	
Visibility (km);	average value for day
Visibility (km);	average value for previous day
Wind speed (knots);	average for day
Wind speed (knots);	average for previous day

Local visibility was estimated at the start of each watch in five categories; 1, excellent ≡ at least 100 km; 2, good ≡ 50 to 100 km; 3, moderate ≡ 20 to 50 km; 4, poor ≡ 5 to 20 km; 5, bad ≡ less than 5 km. The height of the victim above the sea at the start of the chase was estimated in relation to known heights of cliff features at each site, and each chase was categorised into the nearest of four heights; 25, 50, 100 or 200 feet above sea level. The speed of reaction of the victim was scored in three categories. By watching the skuas in the area, it was possible to concentrate on individuals which were actively patrolling rather than soaring to gain height or gliding or flapping to a different position, and to detect the change in skua flight as soon as a victim had been singled out. The speed of reaction was then estimated by watching the victim. If it began evasive action (accelerated flight or dive towards the sea)

as soon as the skua had begun directed flight, reaction speed was "fast" (1). If the victim did not begin evasive action until the skua had almost reached it, reaction was "slow" (3). Intermediate results were scored as "average"(2). Although arbitrary, this scoring was easy to do, and few cases were borderline. A number of chases were not noticed until after the victim had taken evasive action, and these were not recorded. On a number of occasions, skuas were seen to change from patrolling flight to directed flight for a second or two, then to return immediately to patrolling flight. These cases were not considered to be chases, but the borderline between these aborted chases and short unsuccessful chases is an arbitrary and subjective one, which could lead to differences, perhaps of about 10%, in absolute success rates recorded by different people.

It was clear that the two skua species adopt different methods of kleptoparasitism. Arctic Skuas rely on their aerodynamic agility to outmanoevre their victims, and usually initiate a chase from a similar height to the victim, or from slightly above. Most chases begin from behind or to the side of the victim, but it is not uncommon for an Arctic Skua to intercept the path of a victim, so reducing its flight speed. Great Skuas invariably initiate a chase by circling above potential victims, then, when an individual has been selected, stooping at it at very great speed. They appear to rely mainly on surprise to effect a successful robbing, while Arctic Skuas appear to rely mainly on agility and persistence. Victims show two methods of evading skuas. Some, mainly auks, dive into the sea, and once in the sea, the skua always gives up the attack, but others outfly the skua, either by accelerated direct flight (auks) or by ariel contortions (other species).

During the 40 observation periods, 742 chases were recorded

(table 114). There were clear differences in numbers of each species chased by each skua and at each site. Arctic Skuas chased more Arctic Terns at North Hoevdi and more Puffins, Razorbills and Guillemots at East Hoevdi (table 115, $X^2_4 = 182.6$, $p < 0.005$). Great Skuas chased more Razorbills, and possibly more Kittiwakes and Arctic Skuas at North Hoevdi, and more Gannets, and possibly more Puffins and Guillemots at East Hoevdi (table 116), but in view of the small number of chases seen at North Hoevdi, these differences cannot be tested statistically. At North Hoevdi, Arctic Skuas chased large numbers of Arctic Terns, which are not chased by Great Skuas, but chased significantly fewer Puffins or Razorbills (table 117, $X^2_3 = 53.6$, $p < 0.005$). At East Hoevdi, Arctic Skuas chased significantly more Kittiwakes and Puffins than chased by Great Skuas, but significantly fewer gulls, Guillemots or Gannets (table 118, $X^2_6 = 59.9$, $p < 0.005$). The success of chases, measured by whether or not the victim dropped or regurgitated food, varied between species (table 119). Clearly Arctic Skuas chase Arctic Terns and Kittiwakes more often than Great Skuas do because they have a higher probability of success than Great Skuas when chasing these species.

Conversely, Arctic Skuas have very low success rates when chasing Guillemots or Razorbills, and would presumably have even less chance of success in chases of Gannets or gulls if these were to be attempted.

Some reasons for these differences are obvious. The Arctic Tern is too agile to be chased by Great Skuas, and the Kittiwake is usually able to outmanoevre Great Skuas, although Arctic Skuas can more than match the ariel contortions of these species. Auks, particularly the larger species, are less likely to be frightened by the small Arctic Skua than by the much larger and more powerful Great Skua. Auks can evade Great Skuas by diving into the sea, but gulls cannot, so are less

Table 114. Kleptoparasitic chases observed in 1975 and 1976 at two sites on Foula.

	East Hoevdi				North Hoevdi			
	Great Skua		Arctic Skua		Great Skua		Arctic Skua	
Victim	n	%	n	%	n	%	n	%
Arctic Tern	0	0.0	0	0.0	0	0.0	87	74.4
Kittiwake	11	2.4	20	12.7	2	12.5	13	11.1
Puffin	217	48.1	96	60.8	6	37.5	14	12.0
Razorbill	31	6.9	15	9.5	7	43.8	3	2.6
Guillemot	113	25.1	27	17.1	0	0.0	0	0.0
Gannet	69	15.3	0	0.0	0	0.0	0	0.0
Arctic Skua	2	0.4	0	0.0	1	6.3	0	0.0
Great B.-b. Gull	6	1.3	0	0.0	0	0.0	0	0.0
Herring Gull	2	0.4	0	0.0	0	0.0	0	0.0
Totals	451		158		16		117	

Table 115. Kleptoparasitic chases by Arctic Skuas at each site. Expected number of chases if no heterogeneity between sites are given in parentheses.

Victim	East Hoevdi	North Hoevdi
Arctic Tern	0 (50.0)	87 (37.0)
Kittiwake	20 (19.0)	13 (14.0)
Puffin	96 (63.2)	14 (46.8)
Razorbill	15 (10.3)	3 (7.7)
Guillemot	27 (15.5)	0 (11.5)
Totals	158	117

Table 116. Kleptoparasitic chases by Great Skuas at each site. Expected numbers of chases if no heterogeneity between sites are given in parentheses.

Victim	East Hoevdi	North Hoevdi
Kittiwake	11 (12.6)	2 (0.4)
Puffin	217 (215.4)	6 (7.6)
Razorbill	31 (36.7)	7 (1.3)
Guillemot	113 (109.1)	0 (3.9)
Gannet	69 (66.6)	0 (2.4)
Arctic Skua	2 (2.9)	1 (0.1)
"gulls"	8 (7.7)	0 (0.3)
Totals	451	16

Table 117. Kleptoparasitic chases by Great Skuas and Arctic Skuas at North Hoevdi. Expected numbers of chases if no heterogeneity between skuas are given in parentheses.

Victim	Great Skua	Arctic Skua
Arctic Tern	0 (9.9)	87 (77.1)
Kittiwake	2 (1.7)	13 (13.3)
Puffin	6 (2.3)	14 (17.7)
Razorbill	7 (1.1)	3 (8.9)
Totals	15	117

Table 118. Kleptoparasitic chases by Great Skuas and Arctic Skuas at East Hoevdi. Expected numbers of chases if no heterogeneity between skuas are given in parentheses.

Victim	Great Skua	Arctic Skua
Kittiwake	11 (23.0)	20 (8.0)
Puffin	217 (231.8)	96 (81.2)
Razorbill	31 (34.1)	15 (11.9)
Guillemot	113 (103.7)	27 (36.3)
Gannet	69 (51.1)	0 (17.9)
Arctic Skua	2 (1.5)	0 (0.5)
"gulls"	8 (5.9)	0 (2.1)
Totals	451	158

Table 119. Proportions of kleptoparasitic chases which were successful in causing food to be dropped by the victim.

Victim	Great Skua chasing			Arctic Skua chasing		
	number of chases	successful number	%	number of chases	successful number	%
Arctic Tern	0	-	-	87	38	43.7
Kittiwake	13	2	15.4	33	11	33.3
Puffin	223	84	37.7	110	23	20.9
Razorbill	38	7	18.4	18	2	11.1
Guillemot	113	33	29.2	27	3	11.1
Gannet	69	21	30.4	0	-	-
Arctic Skua	3	2	(66.7)	0	-	-
Great Black-backed Gull	6	2	(33.3)	0	-	-
Herring Gull	2	1	(50.0)	0	-	-
Totals	467	152	32.5	275	77	28.0

likely to escape with their food.

To examine in more detail the factors determining success of chases, stepwise multiple regression analyses were carried out. First, all chases by Great Skuas were examined. A total (n) of 467 had been recorded.

Table 120. Statistics from stepwise multiple regression analysis of Great Skua chases of all species, with result of chase the dependent variable. Only relationships for which $p < 0.05$ are included in the table.

Independent variable	b	se (b)	F	R^2
Speed of reaction to skua	0.372	0.031	112.00	0.169
Height of victim above sea	0.006	0.001	72.11	0.282
Local visibility	0.059	0.018	10.98	0.299
Number skuas chasing	0.106	0.046	5.34	0.306
Puffin	0.086	0.037	5.43	0.313
Arctic Skua	0.507	0.226	5.01	0.321

The speed of reaction of the victim accounts for 17% of the variance, and height of the victim another 11%. Success of Great Skua chases is greater the slower the reaction of victims and the higher they are above sea level (table 120). It also increases significantly the worse the visibility around Foula, the more skuas that chase the victim, and, after these factors have been taken into account, if the victim is a Puffin or an Arctic Skua. All these relationships have been assumed to be linear. When this analysis

is repeated including logarithmic transformations of these variables, no significant improvement of R^2 was obtained, so further analyses have been based on assumed linear relationships. The probability of success of chases by Arctic Skuas (number observed (n) = 275) is significantly greater the longer the chase continues, the more slowly the victim reacts, and after allowing for these two factors, the probability of success is significantly lower if the victim is a Kittiwake (table 121).

Table 121. Statistics from stepwise multiple regression analysis of Arctic Skua chases of all species with result as dependent variable. Only relationships for which $p < 0.05$ are included (n = 275).

Independent variable	b	se(b)	F	R^2
Duration of chase	0.042	0.007	34.90	0.143
Speed of reaction to skua	0.149	0.041	13.99	0.185
Kittiwake	- 0.220	0.085	6.74	0.205

The significant differences in success of chases of different species, together with differences in the evasion behaviour of each victim species, suggest that the multiple regression analyses should be carried out separately for each species of victim chased by each skua species.

Great Skua chases of Puffins are more likely to be successful if the Puffin is slow to react, is high above the sea, and if local visibility is bad. These factors explain 36% of the variation in

chase outcome (table 122).

Table 122. Statistics from stepwise multiple regression analysis of Great Skua chases of Puffins with result as dependent variable. Only relationships for which $p < 0.05$ are included ($n = 223$).

Independent variable	b	se(b)	F	R^2
Speed of reaction to skua	0.339	0.044	60.2	0.202
Height of victim above sea	0.006	0.001	49.5	0.336
Local visibility	0.077	0.027	8.5	0.360

Great Skua chases of Razorbills are more likely to be successful if the Razorbill is slow to react ($n = 38$, $b = 0.273$, $se(b) = 0.092$, $F = 8.8$, $R^2 = 0.196$). No other factors show a significant effect, not surprisingly as only 38 such chases were recorded. Great Skua chases of Guillemots are more likely to be successful if the Guillemot is slow to react, is high above the sea, and is chased by more than one skua, and these factors account for 46% of the variance (table 123).

Great Skua chases of Gannets are more likely to be successful if more than one skua is involved in the chase ($n = 69$, $b = 0.194$, $se(b) = 0.094$, $F = 4.3$, $R^2 = 0.060$), but no other factors were significantly related to success. Great Skua chases of "gulls" (i.e. Arctic Skuas, Kittiwakes, Great Black-backed Gulls and Herring Gulls) are more likely to be successful the longer the chase continues ($n = 24$, $b = 0.023$, $se(b) = 0.010$, $F = 4.9$, $R^2 = 0.180$), but no other

Table 123. Statistics from stepwise multiple regression analysis of Great Skua chases of Guillemots (n = 113) with result as dependent variable. Only relationships for which $p < 0.05$ are included.

Independent variable	b	se(b)	F	R^2
Speed of reaction to skua	0.405	0.050	66.9	0.310
Height of victim above sea	0.007	0.002	18.7	0.431
Number skuas chasing	0.455	0.205	4.5	0.456

Table 124. Statistics from stepwise multiple regression analysis of Arctic Skua chases of Puffins (n = 110) with result as dependent variable. Only relationships for which $p < 0.05$ are included.

Independent variable	b	se(b)	F	R^2
Duration of chase	0.046	0.011	15.8	0.157
Speed of reaction to skua	0.147	0.058	6.3	0.204

factors were significantly related to success.

Arctic Skua chases of Arctic Terns are more likely to be successful the longer the chase continues ($n = 87$, $b = 0.049$, $se(b) = 0.013$, $F = 13.5$, $R^2 = 0.137$). Arctic Skua chases of Kittiwakes are also significantly more likely to be successful only if they continue for longer than average ($n = 33$, $b = 0.037$, $se(b) = 0.018$, $F = 4.1$, $R^2 = 0.117$). Arctic Skua chases of Puffins are more likely to be successful the longer it takes the Puffin to react to the skua and the longer the chase continues (table 124).

Arctic Skua chases of Guillemots and Razorbills are more successful the longer it takes the auk to react to the approaching skua ($n = 45$, $b = 0.162$, $se(b) = 0.065$, $F = 6.2$, $R^2 = 0.126$).

The significant factors influencing the outcome of chases can be summarised in an array, classifying the interactions between skua and victim by the factors determining success (table 125). This array suggests that the factors influencing the probability of success vary more between types of victims than between skua species. Thus, persistence seems to be less a quality of the Arctic Skua than a necessary attribute of a skua which attempts to rob a gull or tern. Success in initiating an attack unnoticed by the victim, resulting in a slow reaction speed of the victim, improves the probability of success in eliciting the dropping of food only in auks, and does so for both Great Skuas and Arctic Skuas. The main differences between the skuas is that the Arctic Skua relies on persistence when robbing Puffins, which the Great Skua does not, and the height of auks above the sea does not influence Arctic Skua success but does influence the chances of success of Great Skua chases.

Why then do Arctic Skuas frequently give up chases of Arctic Terns when longer chases are more likely to be successful than shorter

Table 125. The classification of skua-victim interactions by the factors which have a significant influence on the probability of successful robbing.

Victim	Skua	Factors having a significant influence				
		Duration of chase	Speed of reaction to skua	Height of victim above sea	Local Visibility	number of skuas chasing
Arctic Tern	Arctic	x				
Kittiwake	Arctic	x				
"Gulls"	Great	x				
Puffin	Arctic	x	x			
Guillemot/Razorbill	Arctic		x			
Razorbill	Great		x			
Puffin	Great		x	x	x	
Guillemot	Great		x	x		x
Gannet	Great					x

ones? Why do Great Skuas not form groups to chase Guillemots and Gannets to improve their chances of success? Grant (1971) showed that Puffins chased by more than one Arctic Skua gave up fish in 64% of chases, but did so in only 47% of chases by single Arctic Skuas, although this difference is not statistically significant because his sample sizes are small. Hatch (1970) showed a significant increase in success in relation to the number of gulls in gull-tern interactions in Maine, but also showed that the chances of any individual gull obtaining food decreased as the number of gulls increased, as each tern carried only one fish. Andersson (1976) found that Gannets were more likely to regurgitate if chased by more than one Great Skua, but only 8 of 93 recorded chases (8.6%) involved more than one Great Skua. Only five of the 275 chases by Arctic Skuas observed at Foula (1.8%) involved more than one Arctic Skua, and none involved more than two individuals. Of the 467 chases by Great Skuas, 31 involved two skuas, 5 involved three, and 3 involved four birds. In particular, Gannets and gull species showed higher frequencies of chases by more than one skua (tables 126 and 127).

A discriminant analysis was used to determine which variables differ most between chases involving one or more than one skua. This showed that chases involving more than one skua were more likely to be chases of Gannets, were likely to occur late in the breeding season, and were likely to be of longer duration than average (table 128).

The involvement of more than one skua in a chase appears to be a kleptoparasitic strategy only in chases of Gannets by Great Skuas. With other species, shortage of potential victims appears to be the main cause, as this will tend to occur towards the end of the season, and presumably results in the same victim being selected by more than one skua. The relationship with chase duration probably arises in

Table 126. Numbers of Arctic Skuas involved in chases of each victim recorded at Foula in 1975 and 1976.

Victim	Number of skuas chasing				Percentage of chases with more than one skua.
	1	2	3	4	
Arctic Tern	83	4	0	0	5 %
Kittiwake	33	0	0	0	0 %
Puffin	109	1	0	0	1 %
Razorbill	18	0	0	0	0 %
Guillemot	27	0	0	0	0 %
All victims	270	5	0	0	1.8 %

Table 127. Numbers of Great Skuas involved in chases of each victim recorded at Foula in 1975 and 1976.

Victim	Number of skuas chasing				Percentage of chases with more than one skua involved.
	1	2	3	4	
Kittiwake	11	1	1	0	15 %
Puffin	207	14	1	1	7 %
Razorbill	37	1	0	0	3 %
Guillemot	110	3	0	0	3 %
Gannet	55	11	2	1	20 %
Arctic Skua	3	0	0	0	(0 %)
Great B.-b. Gull	4	1	1	0	(33 %)
Herring Gull	1	0	0	1	(50 %)
All victims	428	31	5	3	8.4 %

Table 128. SPSS discriminant analysis statistics showing factors which differ significantly between chases by one and chases by more than one skua.

Variable entered (stepwise)	Rao's V	Change in Rao's V	Significance of change in Rao's V
Gannet	29.2	29.2	$p < 0.001$
Date	44.1	14.9	$p < 0.001$
Duration	55.7	11.6	$p < 0.001$

the same way; the longer the chase continues the more chance there is that the victim will pass another patrolling skua which will also attack it.

Probably the main advantage to an individual joining a chase is the reduction of the amount of time required in patrolling to select a victim to chase. Patrolling may continue for up to ten minutes before a chase is initiated, so the opportunity to join a chase of a Gannet, with little consequent reduction in the chances of obtaining a fish but with a saving of up to ten minutes patrolling time makes group chasing worthwhile, particularly if patrolling time is long as it is towards the end of the season when potential victims, particularly auks, are scarce.

Great Skua chases of Puffins and Guillemots were more likely to be successful if the victim was high above the sea. This appears to result from the two mutually exclusive methods of evasion available to auks. Sometimes auks dive into the sea to avoid skuas, and sometimes they fly as fast as possible in a straight line, but losing height to accelerate. The two strategies are exclusive because the auks do not appear to be able to hit the sea safely at high speed. Whether or not the auk dives depends partly on its height above the sea when the chase begins; if too high it cannot reach the sea without having to accelerate to keep ahead of the chasing skua. Stepwise multiple regression analyses with method of evasion as dependent variable show that the tendency to dive is greater when the victim is low above the sea and when it is slow to react to the skua (table 129).

The tendency for short chases of Razorbills to result in the victim diving may simply be due to chase duration and speed of reaction being correlated variables. The tendency for Puffins chased

Table 129. Statistics from stepwise multiple regression analyses of kleptoparasitic chases with method of evasion as dependent variable. Only relationships for which $p < 0.05$ are included.

Skua	Victim	Independent variable	b	se(b)	F	R^2
Great	Puffin	Height above sea	- 0.005	0.001	21.5	0.089
Great	Razorbill	Chase duration	- 0.062	0.022	7.7	0.186
		Height above sea	- 0.006	0.003	5.3	0.293
Great	Guillemot	Speed of reaction to skua	0.201	0.064	9.8	0.091
		Height above sea	- 0.005	0.002	5.2	0.132
Arctic	Puffin	Chases per hour	- 0.026	0.011	5.6	0.042
		Height above sea	- 0.005	0.002	4.8	0.084
Arctic	Razorbill/Guillemot	Speed of reaction to skua	0.204	0.074	7.6	0.133
Great	Gannet	Number skuas chasing	0.166	0.077	4.6	0.065

by Arctic Skuas to be more likely to dive the fewer Arctic Skua chases occur per hour, may be a chance correlation or may indicate greater caution on the part of the Puffins the more Arctic Skuas there are in the vicinity. The latter was found by Grant (1971) so is a plausible hypothesis. Diving is resorted to more often if the victim is slow to react to the skua, and this implies that it is not the preferred method of evasion. If the auk can safely outfly the skua this is preferable because it will reach its breeding site quickly to deliver its load of food. By diving into the sea it risks injury, risks the loss of fish due to impact with the water, and loses time in having to swim, surface and take off again. Confirmation of this is found in the proportions of auks which dive if chased by Great Skuas or by Arctic Skuas. As would be expected, Great Skuas elicit diving in a higher proportion of their chases (table 130, overall $X^2_3 = 74.1$, $p < 0.005$).

Not only do Arctic Skuas elicit diving in fewer cases than Great Skuas in chases of each auk species, but both species elicit a higher incidence of diving escape behaviour from the smaller auks, suggesting that Guillemots are less frightened by skua attacks than are Puffins.

The speed of reaction of auks is an important determinant of chase success, and, in the case of Guillemots, influences their method of evasion. The main factor determining the speed of reaction appears to be visibility. Local visibility correlated most closely with speed of reaction in Great Skua - Puffin, Great Skua - Guillemot, Arctic Skua - Puffin, Arctic Skua - Guillemot/Razorbill and Arctic Skua - Kittiwake interactions, while visibility measured at Lerwick Observatory which is of course correlated with visibility estimated in arbitrary categories at Foula ($r = - 0.567$), gave a statistically better fit in Great Skua-Razorbill interactions, although local visibility is

Table 130. Numbers of chases of auks by Great Skuas and by Arctic Skuas which result in the victim diving into the sea to escape.

Victim	Skua	Number of chases.	% dive	Number which dive into sea	Number which outfly skua	χ^2_1
Puffin	Great Skua	223	70.4	157	66	
Puffin	Arctic Skua	110	38.2	42	68	31.7 ($p < 0.005$)
Razorbill	Great Skua	38	81.6	31	7	
Razorbill	Arctic Skua	18	22.2	4	14	18.1 ($p < 0.005$)
Guillemot	Great Skua	113	67.3	76	37	
Guillemot	Arctic Skua	27	14.8	4	23	24.3 ($p < 0.005$)

presumably the controlling influence in this case too. In Great Skua - "gull", Great Skua - Gannet and Arctic Skua - Arctic Tern interactions no variables measured showed a significant relationship with speed of reaction of the victim (table 131).

Again there is the suggestion that the rate of kleptoparasitic chases may affect behaviour of potential victims, as Kittiwakes are significantly faster to react to approaching Arctic Skuas the more chases occur per hour, which is approximately equivalent to the number of Arctic Skuas patrolling per hour.

Chase duration is an important determinant of success in Arctic Skua chases of Arctic Terns, Kittiwakes and Puffins, and in Great Skua chases of "gulls". Analyses by stepwise multiple regression of factors influencing chase duration showed that Great Skua chases are longer if the victim is a Gannet, Great Black-backed Gull, Arctic Skua, Kittiwake or Herring Gull, and if the chase begihs high above the sea (table 132).

Arctic Skua chases are longer if the victim is a Kittiwake or Arctic Tern, if the victim is slow to react, or is high above the sea (table 133).

There are clear differences in the duration of chases of different species, and indications that these may be modified by different factors, so each skua-victim interaction was examined again. Great Skua chases of Puffins and Guillemots were significantly longer if the victim was high above the sea. Great Skua chases of Razorbills were significantly longer if the victim did not dive into the sea, suggesting the same basic relationship in all three auks. No factors were significant in explaining chase duration of Gannets or "gulls". Arctic Skua chases of Arctic Terns, Kittiwakes and Puffins were longer on occasions when the victim was slow to react, and chases of Puffins

Table 131. Statistics from SPSS stepwise multiple regression analyses of kleptoparasitic chases with REACT (speed of reaction of the victim) as the dependent variable.

Skua	Victim	Independent variable	B	se(b)	F	R^2
Great Skua	Puffin	Local visibility	0.152	0.039	14.8	0.063
Great Skua	Razorbill	Visibility at Lerwick	- 0.013	0.006	4.6	0.113
Great Skua	Guillemot	Local visibility	0.204	0.056	13.0	0.105
Arctic Skua	Puffin	Local visibility	0.179	0.050	12.8	0.106
Arctic Skua	Guillemot/Razorbill	Local visibility	0.240	0.085	7.9	0.157
Arctic Skua	Kittiwake	Local visibility	0.187	0.053	12.6	0.295
		Arctic Skua chases per hour	- 0.018	0.008	5.0	0.392

Footnote: Local visibility score <u>decreases</u> as visibility at observatory <u>increases</u>

Table 132. Statistics from SPSS stepwise multiple regression analysis of chases of all victims by Great Skuas, with chase duration as the dependent variable (n = 467).

Independent variable	B	se(B)	F	R^2	change in R^2
GANNET	8.991	0.542	275.5	0.304	0.304
G.B.B. GULL	10.245	1.658	38.2	0.349	0.045
ARCTIC SKUA	13.945	2.311	36.4	0.389	0.041
HEIGHT ABOVE SEA	0.035	0.008	20.9	0.411	0.022
KITTIWAKE	4.839	1.129	18.4	0.435	0.023
HERRING GULL	7.553	2.920	6.7	0.448	0.014

Table 133. Statistics from SPSS stepwise multiple regression analysis of chases of all victims by Arctic Skuas, with chase duration as the dependent variable (n = 275).

Independent variable	B	se(B)	F	R^2	change in R^2
KITTIWAKE	5.990	0.635	89.1	0.225	0.225
ARCTIC TERN	1.222	0.501	6.0	0.318	0.093
SPEED OF REACTION	1.711	0.327	27.5	0.363	0.045
HEIGHT ABOVE SEA	0.028	0.008	11.0	0.394	0.032

were also longer if the victim was high above the sea (table 134).

Combining the results obtained above, the actions of factors which modify the chances of success of chases can be illustrated as in figure 43. In no case did wind speed show any influence on chase outcome, but visibility is clearly important, such that Great Skuas are considerably more likely to be successful in misty conditions, but Arctic Skuas only slightly more successful because they rely less on surprise than on persistence, and slow reaction of the victim mainly improves the chances of the skua getting close enough to its victim to allow a prolonged chase. Given this relationship with visibility, the form of any relationship between local visibility and the mean number of chases per hour might be predicted. Great Skuas should show an increase in chase rate in poor visibility caused by larger numbers of birds indulging in kleptoparasitism, because it is a more profitable strategy under these conditions, and also because locating feeding flocks at fish shoals becomes more difficult if visibility is not good. Arctic Skua chase rates should not be greatly influenced by visibility as they have no alternative food source. Both skuas show correlations between chase rates and time in the breeding season, owing to seasonal changes in food requirement and availability, so partial correlation coefficients between visibility and chase rate must be calculated, allowing for the influence of date on chase rate. Doing this gives partial correlation coefficients between chase rates and visibility which are not statistically significant for either species, but suggest that Great Skuas may be slightly more active in kleptoparasitising during misty conditions as predicted. The relationship is so weak however (table 135), that other factors must have an overriding effect. Possibly fish availability, which varies sporadically both spatially and temporally, has a

Table 134. Statistics from SPSS stepwise multiple regression analyses of kleptoparasitic chases with DUR (chase duration) as the dependent variable.

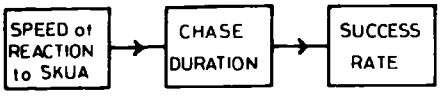
Skua	Victim	Independent variable	B	se(B)	F	R^2
Great Skua	Puffin	Height above sea	0.036	0.006	38.4	0.148
Great Skua	Guillemot	Height above sea	0.027	0.012	5.3	0.046
Great Skua	Razorbill	Method of evasion	- 2.765	0.963	8.2	0.186
Arctic Skua	Arctic Tern	Speed of reaction	2.104	0.654	10.3	0.109
Arctic Skua	Kittiwake	Speed of reaction	3.969	1.723	5.3	0.146
Arctic Skua	Puffin	Height above sea	0.066	0.012	28.3	0.185
		Speed of reaction	1.236	0.431	8.2	0.243

Table 135. Correlations between chase rates and date, chase rate and local visibility, and chase rate and local visibility controlling for the variation due to date.

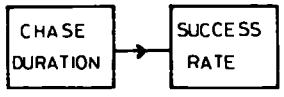
Correlation	Great Skua	Arctic Skua
Between chase rate and date	0.405 (p = 0.008)	- 0.139 (p = 0.212, ns)
Between chase rate and local visibility	0.209m (p = 0.114, ns)	0.101 (p = 0.281, ns)
Between chase rate and local visibility (controlling for date)	0.243 (p = 0.080, ns)	0.098 (p = 0.291, ns)

Figure 43. Factors which significantly influence ($p < 0.05$) the probability of success of kleptoparasitic chases of seabird species by Great and Arctic Skuas. Relationships were determined by stepwise multiple regression.

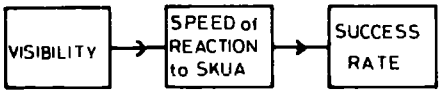
ARCTIC SKUA ; TERN or KITTIWAKE



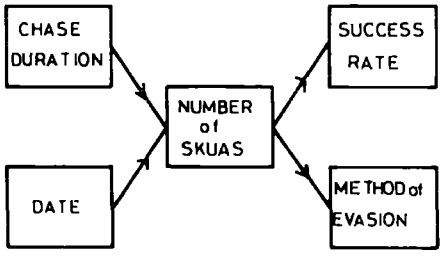
GREAT SKUA ; LARUS spp.



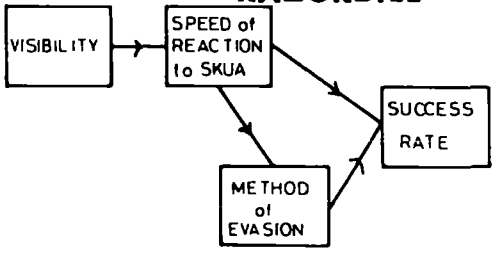
GREAT SKUA ; RAZORBILL



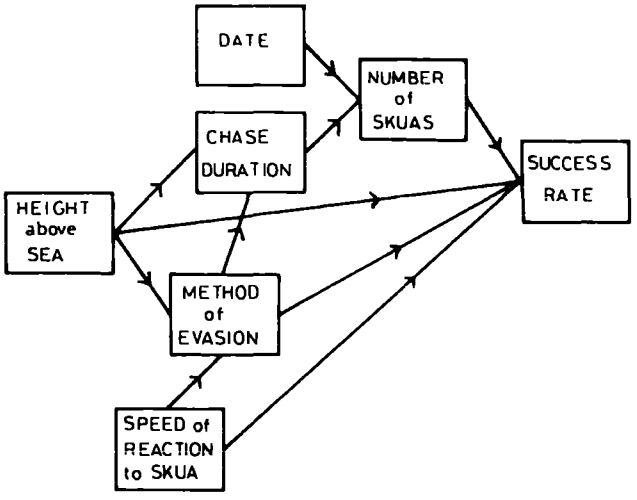
GREAT SKUA ; GANNET



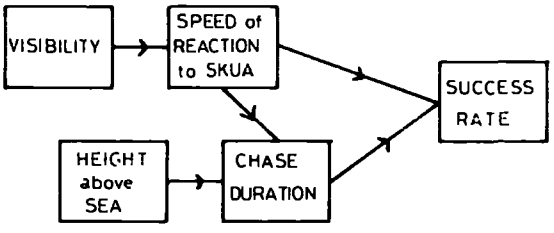
ARCTIC SKUA ; GUILLEMOT or RAZORBILL



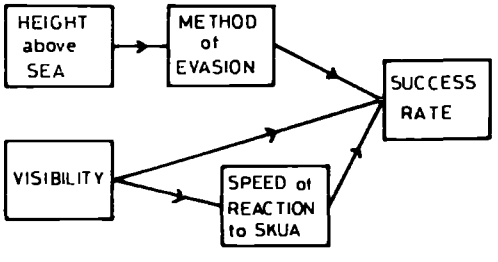
GREAT SKUA ; GUILLEMOT



ARCTIC SKUA ; PUFFIN



GREAT SKUA ; PUFFIN



greater influence than weather conditions.

The mean number of sandeels obtained per chase is shown for each skua-victim interaction in table 136. Both skuas obtain slightly less than 0.5 fish per chase. Arctic Skuas usually return to their territory with a load consisting of between one and six sandeels, so must average between two and 14 chases per feeding trip, which would require between 14 and 38 chases to obtain. The amount of patrolling time required to make these numbers of chases further indicates that kleptoparasitic activity must occur close to Foula.

The considerable difference in the preferred victims of each skua species (table 136) suggests that very little competition occurs between the species for food taken by kleptoparasitism, and only late in the season is there evidence of a shortage of potential victims (resulting in some multiple chases) by which stage Arctic Skuas will almost all have fledged their young.

Effects of interspecific competition for territories

The Great Skua appears to have had little effect on Arctic Skua numbers, and little effect on food availability to Arctic Skuas, but it has limited the area available to Arctic Skuas for nesting, resulting in increased nest densities, and breeding in habitats which were previously not used. The changes in the distribution of colonies has been most pronounced on Foula, Hermaness and Noss, and these colonies are shown in figures 44 to 54. In each colony map, occupied areas of Great Skua colony are shown by vertical bars, Arctic Skua colonies on Foula and Hermaness by horizontal bars, and on Noss by stippling, and the Arctic Tern colonies on Foula by solid black. In the habitat maps (figures 44, 48 and 52), areas of marginal cultivation or active

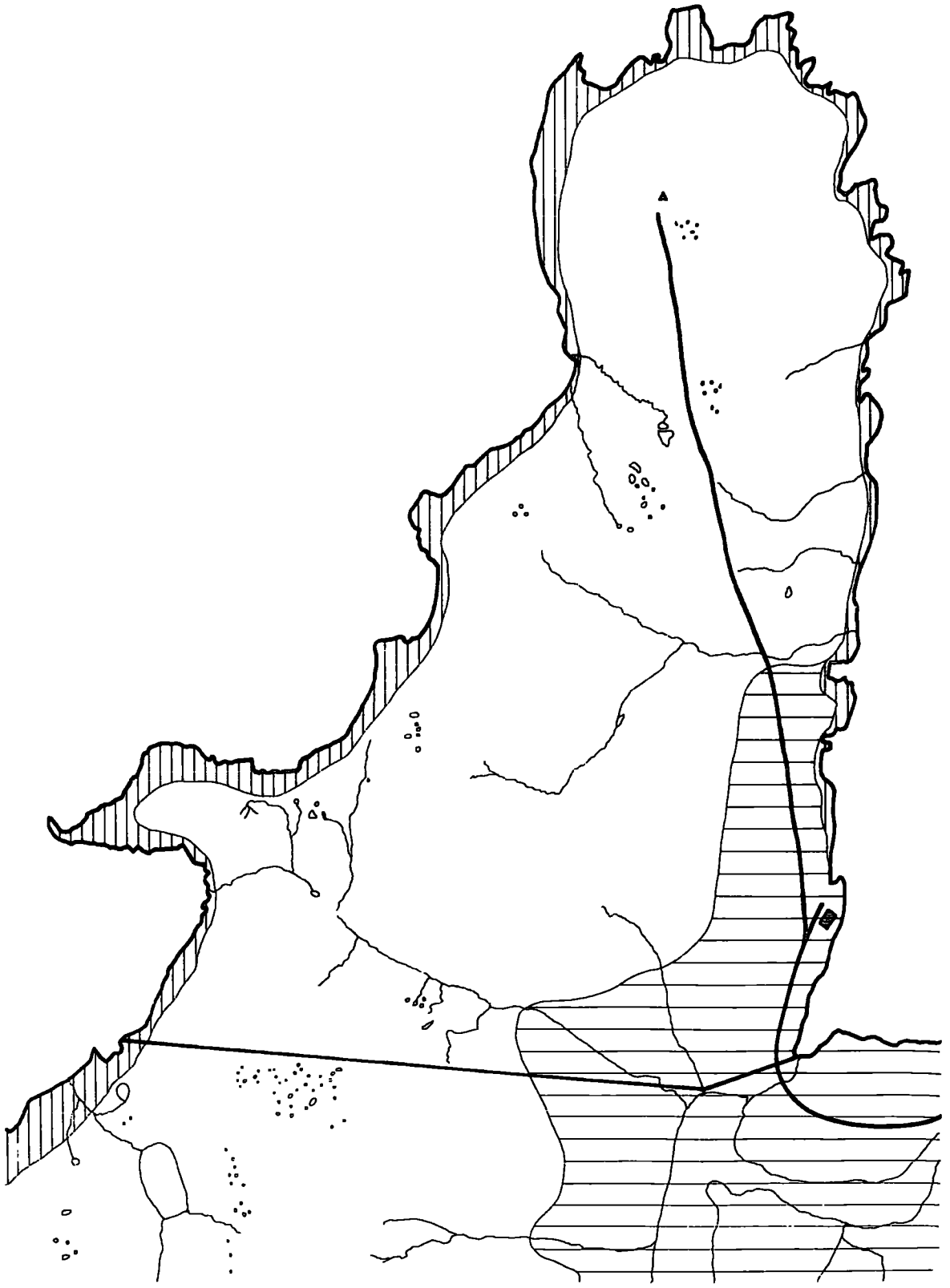
Table 136. Mean numbers of fish obtained from chases of different species by Great and Arctic Skuas. (Number of chases in parentheses).

Skua	Victim	Mean number of fish obtained per chase.		Standard error
Arctic Skua	All victims	(275)	0.393	0.042
	Arctic Tern	(87)	0.437	0.053
	Kittiwake	(33)	0.727	0.196
	Puffin	(110)	0.373	0.072
	Razorbill	(18)	0.111	0.076
	Guillemot	(27)	0.111	0.062
Great Skua	All victims	(467)	0.488	0.039
	Kittiwake	(13)	0.308	0.208
	Puffin	(223)	0.543	0.053
	Razorbill	(38)	0.184)	0.064
	Guillemot	(113)	0.257	0.041
	Gannet	(69)	0.812	0.159
	Arctic Skua	(3)	1.667	0.882
	Great B.-b. Gull	(6)	0.667	0.422
	Herring Gull	(2)	1.000	1.000

peat diggings are marked by horizontal bars, clifftop grassland by vertical bars and "scalped peat" by stippling. "Scalped peat" areas are found only on Foula and are areas where the inhabitants have dug all the peat away from the bedrock, so that there is only a thin cover of lichens, grasses and short growths of Empetrum growing in peat dust between stones and gravel. With increases in numbers of Great Skuas, Arctic Skuas have been forced to move to areas of cliff-top grassland, of marginal cultivation and scalped peat (figures 47, 51 and 54), although when nesting space was unlimited both skuas showed a clear tendency to avoid holding territories in such areas (figures 45 and 49). Arctic Skuas have also tended to become concentrated in areas of active peat digging and along paths, where human disturbance is frequent and serious. They have also began to nest in close association with tern colonies, where they derive some protection from interference by Great Skuas through the mobbing behaviour of the terns. A further tendency is for Arctic Skua colony areas to have become fragmented into disjunct individual territories, often bounded by Great Skua territories on one side and an unsuitable habitat on the other.

Estimates of Arctic Skua nest density on Unst (table 109) and on Foula (table 110), suggest that Arctic Skuas chose to nest at a density of between 25 and 30 pairs km^{-2} when space is not limited. Presumably this density is optimal for breeding. Increases in Great Skua numbers have compressed Arctic Skuas into densities of up to 218 km^{-2} as on Foula in 1976 (table 110), and this is the highest recorded overall density for any Arctic Skua colony. The breeding success of Great Skuas nesting in high density areas of Foula is significantly lower than that of birds of comparable experience nesting at lower densities (section 5): most of the reduction is caused by intraspecific conflict

Figure 44. Distribution of habitats at Hermaness, Unst. Areas of marginal arable land are marked by horizontal bars, areas of clifftop "grassland" by vertical bars and blanket bog is unmarked. The main path to the summit (marked ▲) is shown by a heavy line, as is the boundary of the reserve.



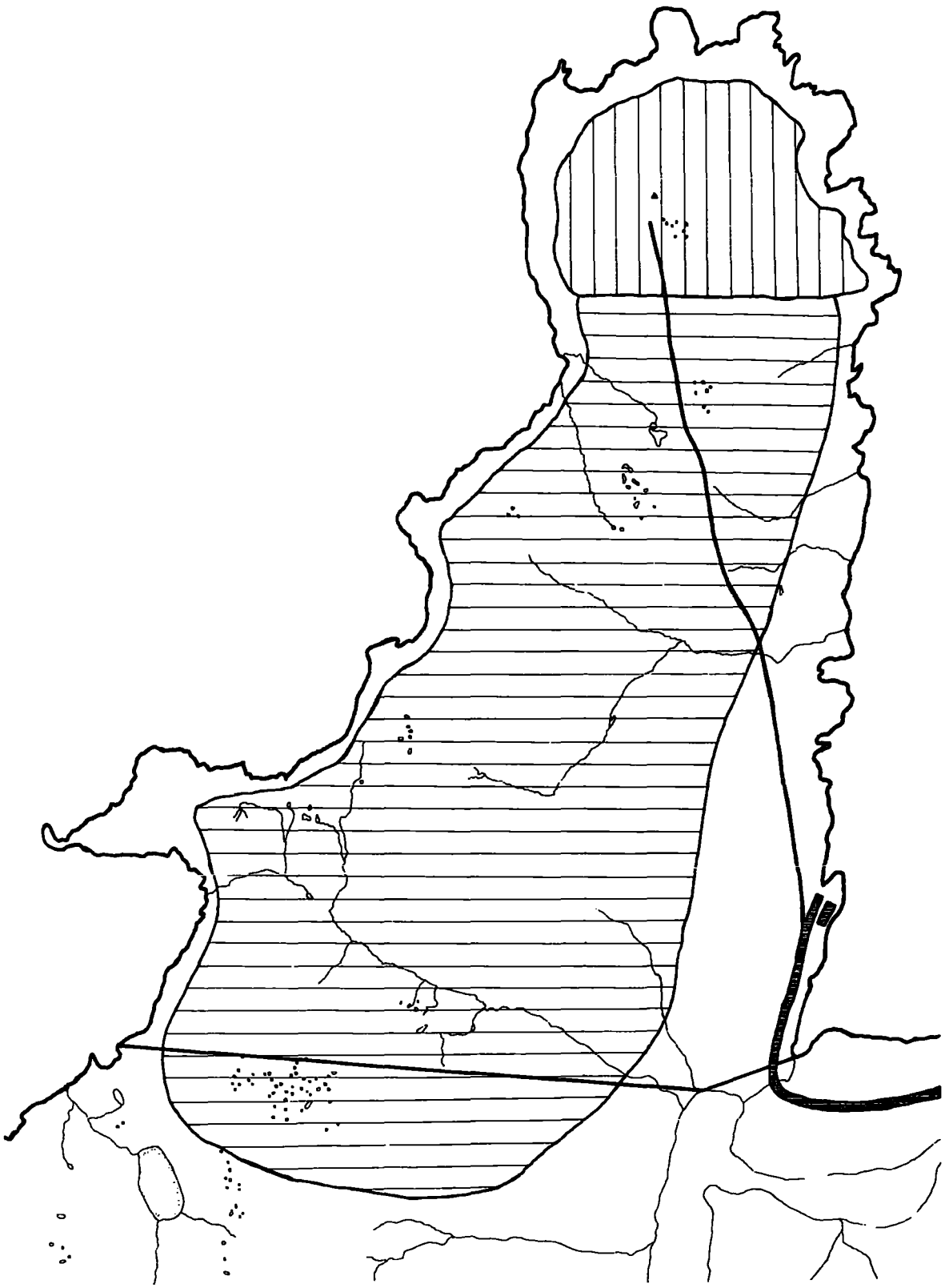
Figures 45, 46, and 47. Distribution of Great Skua and Arctic Skua territories at Hermaness. Great Skua areas are marked by vertical bars and Arctic Skua areas by horizontal bars.

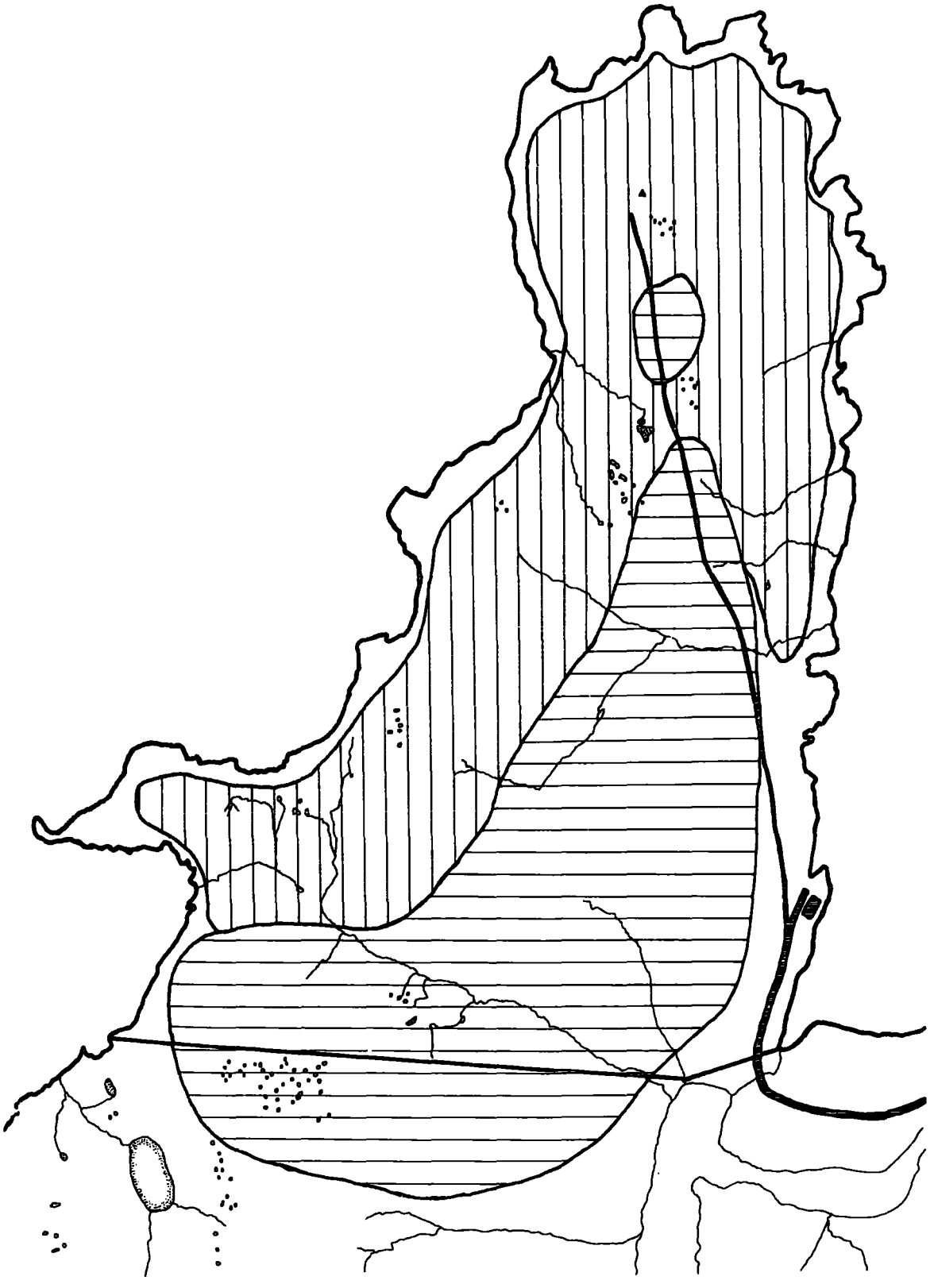
Figure 45: Distributions in 1922 (from Lockie 1950)

Figure 46: Distributions in 1950 (from Lockie 1950)

Figure 47: Distributions in 1975

The Arctic Skua has been pushed into marginal arable areas, areas of clifftop grassland and to areas of human activity, as the Great Skua has spread.





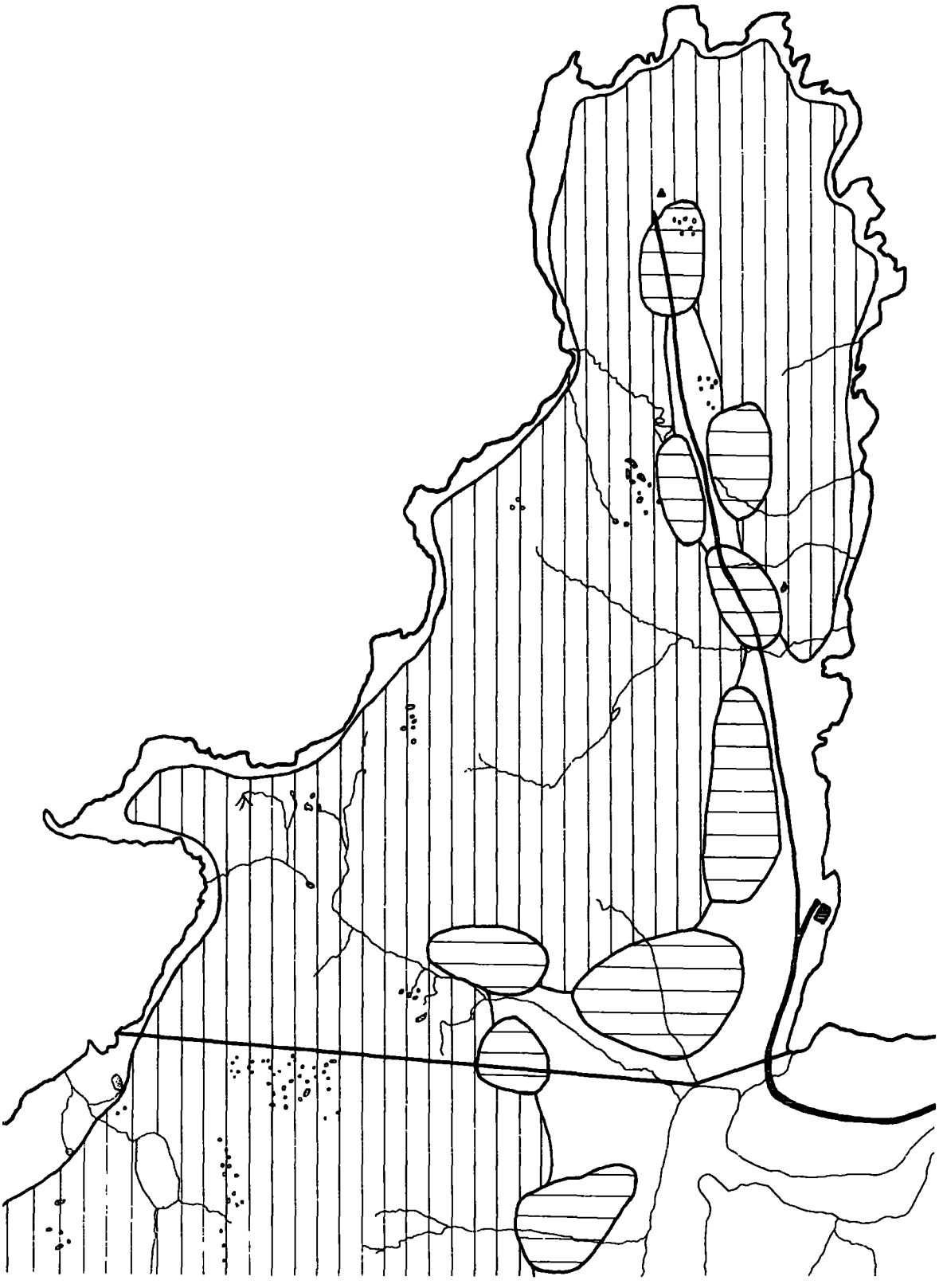
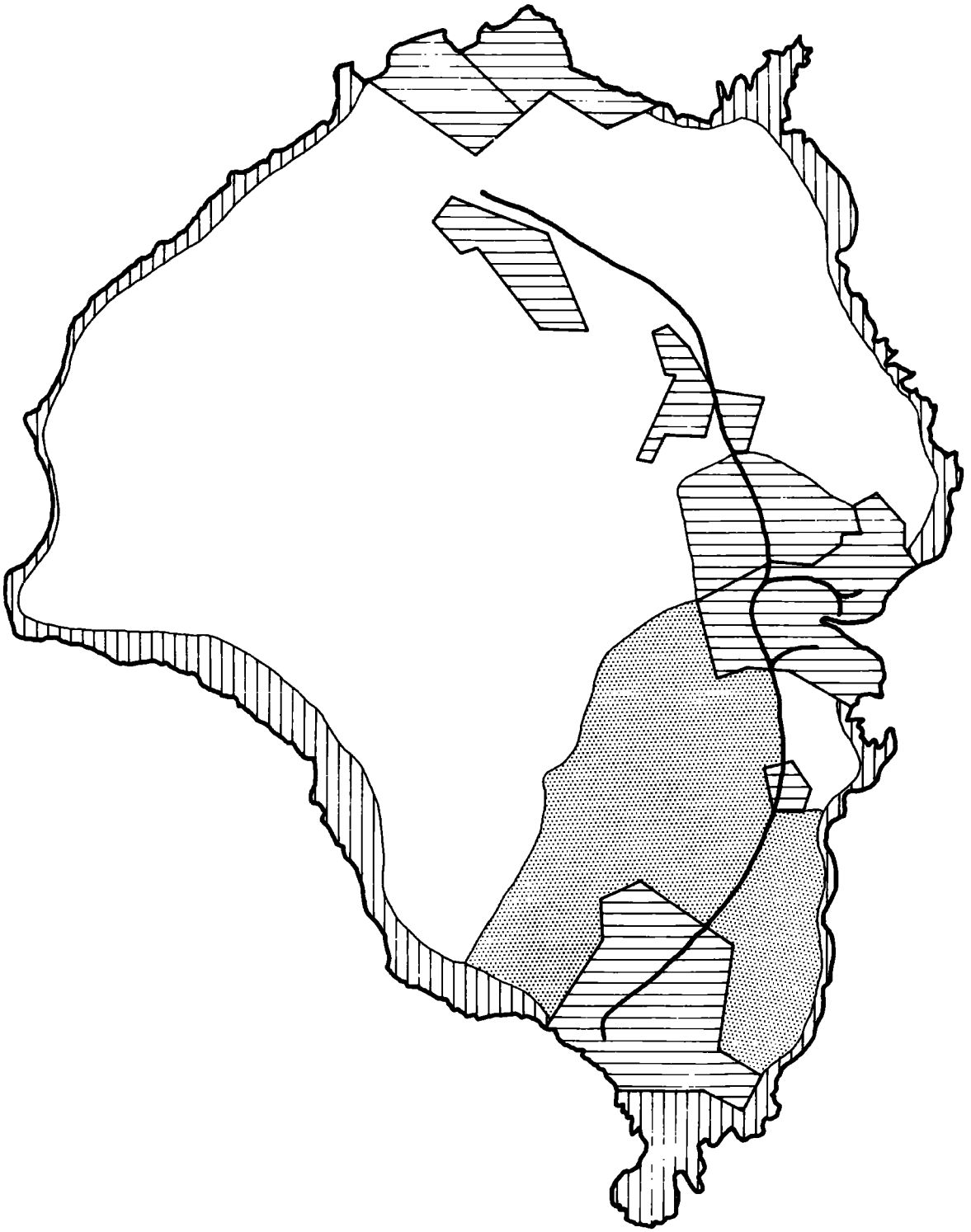


Figure 48. Distribution of habitats at Foula. Crofted or formerly crofted areas are marked by horizontal bars, areas of clifftop grassland by vertical bars, areas of scalped peat, where peat has been dug down to bedrock for burning, by heavy stippling and roads by heavy lines. Unmarked areas are blanket bog.

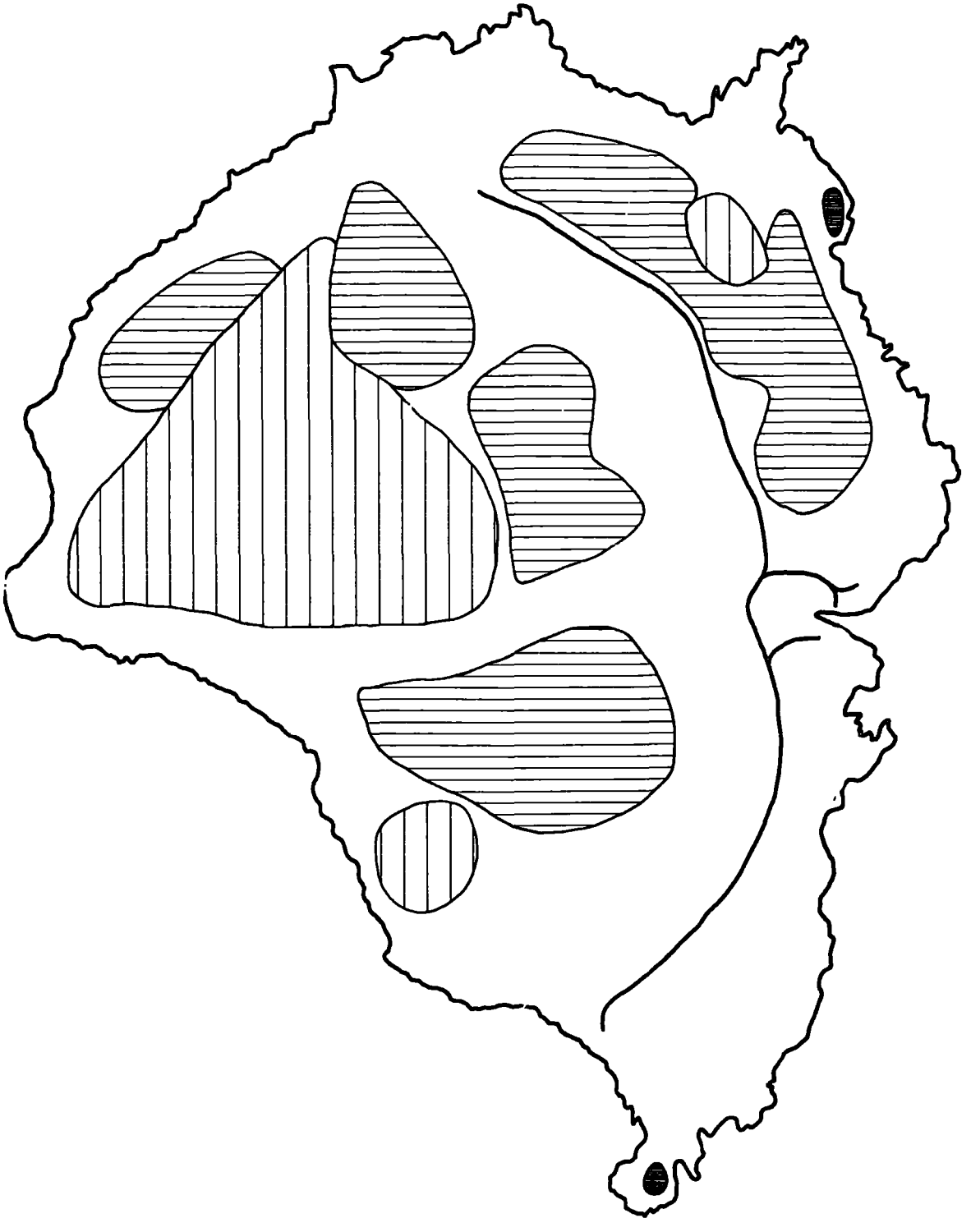


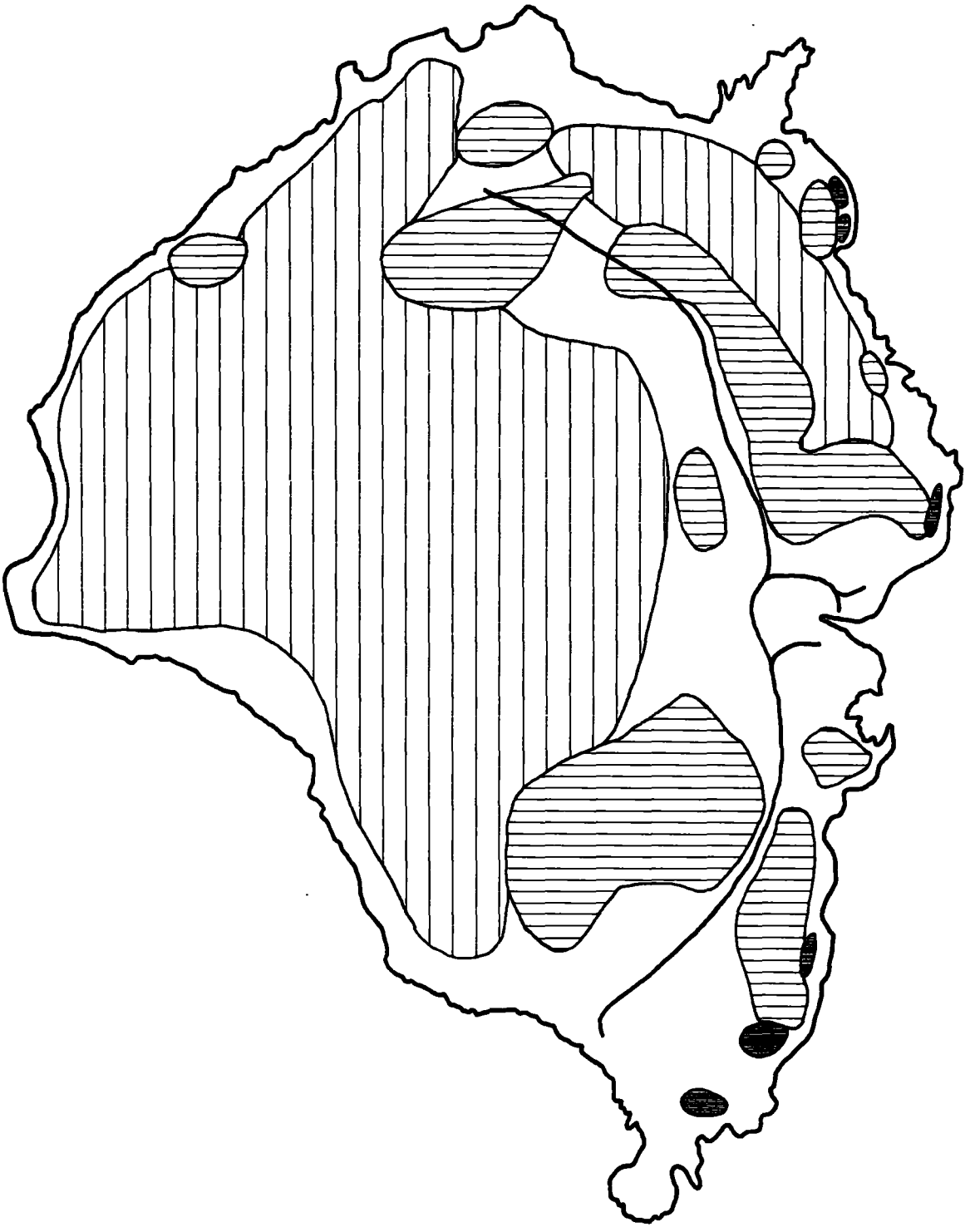
Figures 49, 50 and 51. Distribution of Great Skua, Arctic Skua and Arctic Tern territories at Foula. Great Skua areas are marked by vertical bars, Arctic Skua areas by horizontal bars, and Arctic Tern areas by solid black shading.

Figure 49: Distributions in 1938

Figure 50: Distributions in 1969

Figure 51: Distributions in 1975.





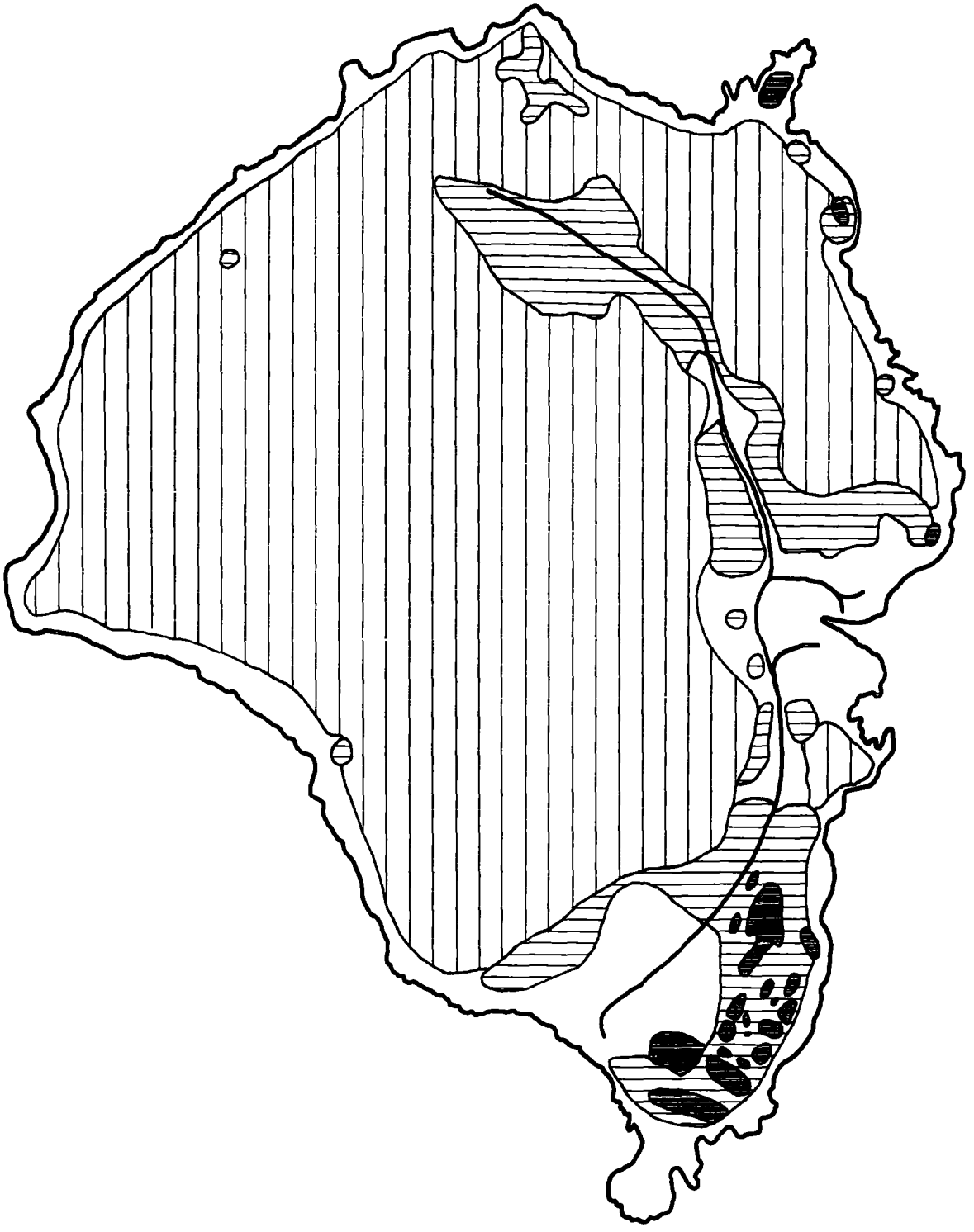
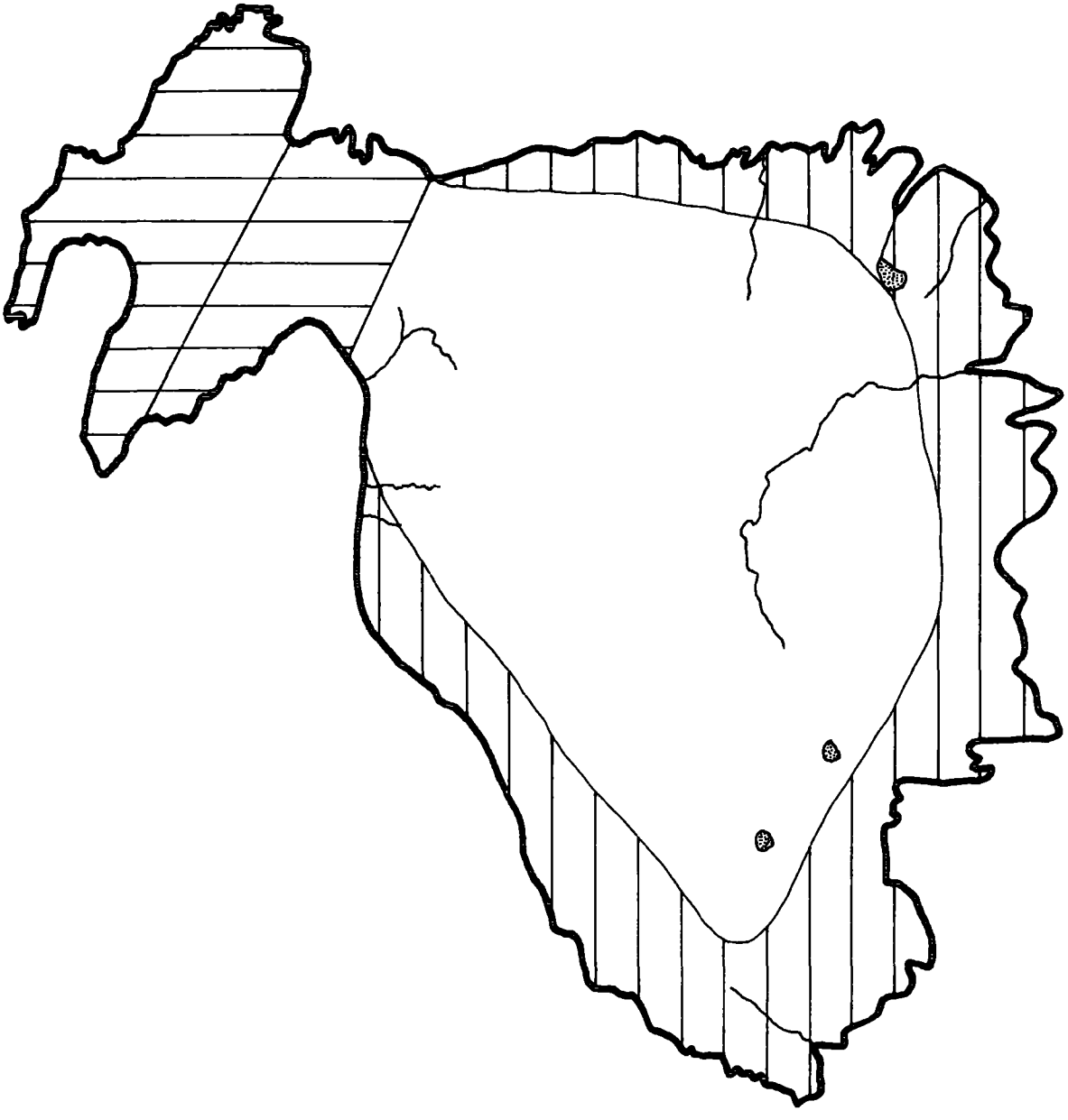


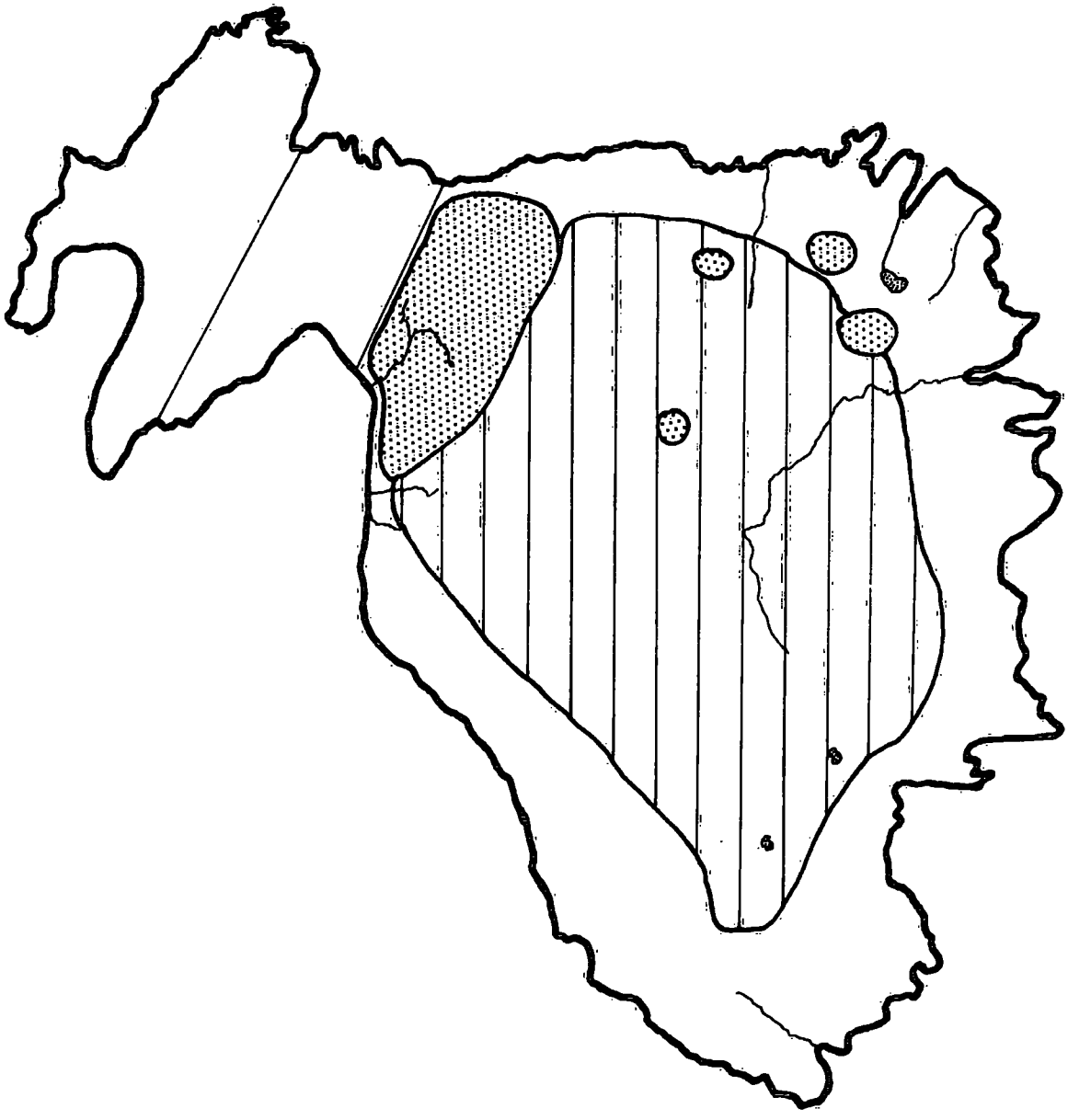
Figure 52. Distribution of habitats at Noss. Crofted or formerly crofted areas are marked by horizontal bars, areas of clifftop grassland by vertical bars, and blanket bog is unmarked.

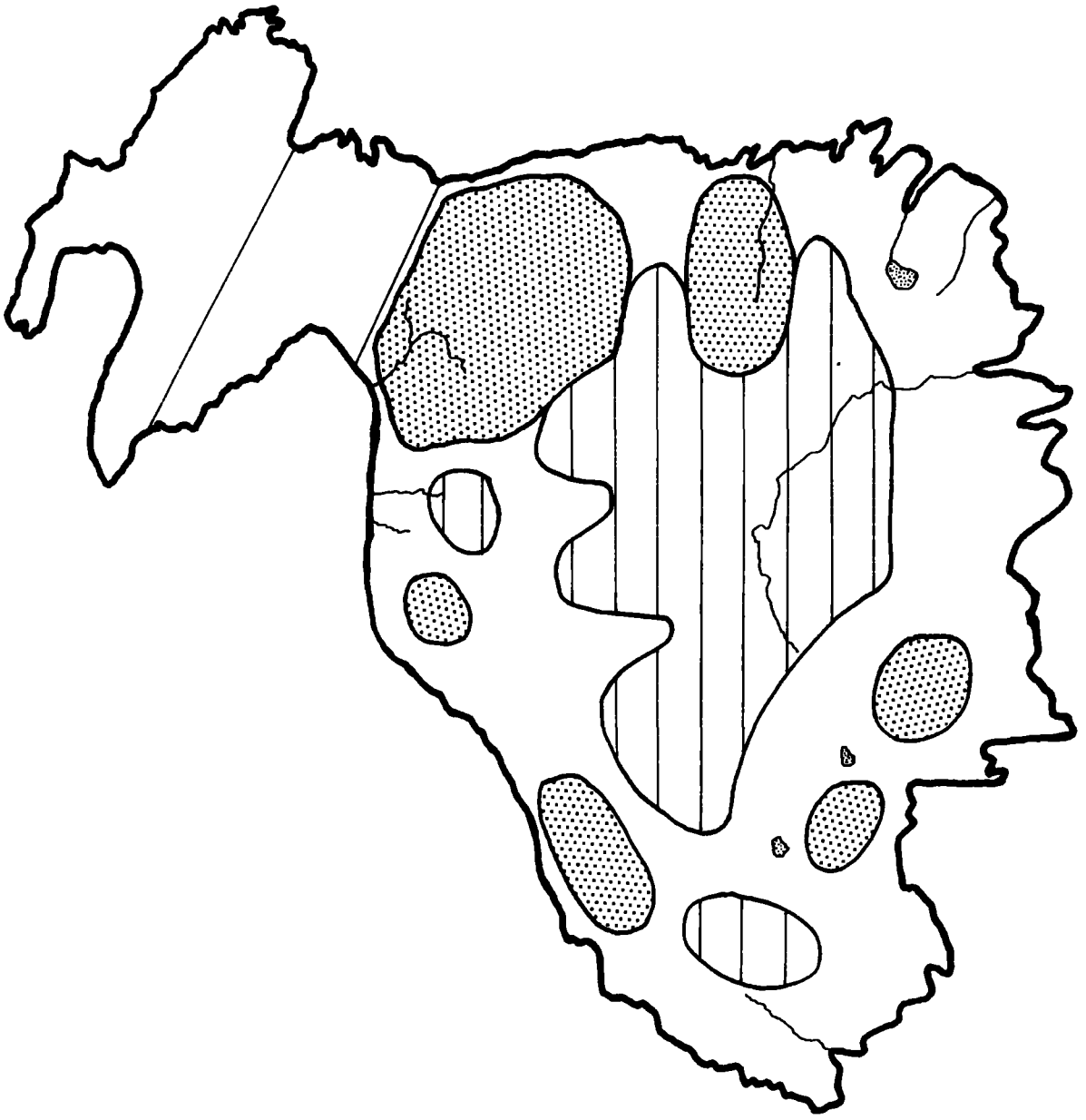


Figures 53 and 54. Distribution of Great Skua and Arctic Skua territories on Noss. Great Skua areas are marked by vertical bars and Arctic Skua areas by heavy stippling.

Figure 53: Distributions in 1946 (from Perry 1948)

Figure 54: Distributions in 1974 (from Kinnear 1974)





between neighbouring pairs, which often results in loss of eggs. A similar reduction in breeding success at high density may be expected for the Arctic Skua, but, because young birds tend to be less successful breeders (e.g. Coulson 1966, 1972) and also hold smaller territories (Davis & O'Donald 1976), it is difficult to isolate the effects of density. No satisfactory estimates of breeding success in relation to density were obtained from Foula, but figures exist for Noss. Breeding success was measured in 1946, when nest density was not much higher than in colonies free from the influences of Great Skuas, and in 1974, when nest density was higher than in any other Arctic Skua colony at that time. In 1946, with a nest density of 62 km^{-2}, 80% of all eggs hatched (Perry 1948). In 1974, when nest density was 157 km^{-2} only 65% of all eggs hatched (Kinnear 1974). Most of the reduction was due to losses of eggs to other Arctic Skuas, but chick mortality before fledging was thought to be similar in both studies (Kinnear 1974). Great Skuas were not believed to have had any great direct effect on breeding success, as they were never seen to take Arctic Skua eggs, and rarely attacked unfledged chicks.

Thus, indirect effects of competition with Great Skuas result in increased nest density, with consequent increased self-induced egg losses, result in nesting in poor quality territories, often subject to human disturbance so likely to have a lower fledging success, and direct predation of fledglings and killing of adults is added to these effects to further reduce Arctic Skua productivity and survival. The mean rate of predation on Arctic Skua fledglings at Hermaness has recently been estimated at 50% (Martin in litt.), which is twice as high as found on Foula. This may be due to the more scattered nature of Arctic Skua territories on Hermaness, allowing Great Skuas to approach without being attacked by adjacent Arctic Skuas, and also to

the greater human disturbance by visitors to the reserve who pass through most of the Arctic Skua territories (figure 51).

The increase in the number of Arctic Skuas on Foula between 1973 and 1976 occurred especially in the vicinity of the Arctic Tern colony south of Ham (figure 47), and resulted in a particularly high nest density in that area (table 137). North of Ham, there are very few Arctic Terns nesting and the Arctic Skua territory size is larger. This suggests that the proximity of the large tern colony, which developed from only 400 pairs before 1970 to 6000 pairs in 1975 (Furness 1977b), may compensate for the disadvantages of small territory size.

Table 137. Territory densities of Arctic Skuas in areas of Foula in 1975.

Area	Pairs	Area (km^2)	Density (pairs km^{-2})
Scattered pairs	30	0.30	100
North of Ham	90	0.88	102
South of Ham	120	0.57	211

Since most of the reduction in breeding success resulting from nesting at high density is caused by intraspecific conflict, there may be a considerable advantage to pairs which spend most of their time in the territory, since they will be able to defend their nests against intruders. The big tern colony may provide a large amount of easily obtained food; a pair nesting in this area can therefore minimise the

amount of time during which the territory is defended by only one adult.

To detect the effects of the location of the territory on Foula, 24-hour watches of three breeding pairs of Arctic Skuas were carried out between 17 and 24 July 1976 with the help of members of a Brathay expedition. As found with the Great Skua, there is a sexual dimorphism in behaviour, although less pronounced, with males foraging more than females (tables 138, 139 and 140), and, as with the Great Skua, the pair coordinate their activities so that the chicks are guarded by at least one parent all the time (table 141).

Although all the fish which were fed to chicks were positively identified, and were all sandeels, fish lengths could not always be seen. The Arctic Skua pairs at Mucklegrind and Ristie fed their chicks as soon as they returned to the territory, or they did not feed them at all but retained any fish obtained on that trip for themselves. As a result, the number of feeds taken by the chick of each of these pairs can be counted. In contrast, the Arctic Skua pair at the Airstrip behaved as Great Skuas do, and gave food which had been retained by the adult for some time after the return to the territory.

All three pairs watched were deliberately chosen to comprise one light phase and one dark or intermediate phase adult to simplify identification of the two adults. Sex was determined by observing mating behaviour early in the season. It is known that light phase birds are later nesting and less productive than dark phase birds, at least in their first breeding season, and these pairs, which oppose the normal trend for assortative mating (Davis & O'Donald 1976), may not be well suited combinations; certainly all three pairs were late nesters, and the watches were carried out at a time when many pairs of Arctic Skuas had almost completed their breeding season, so may not be typical of the species for these reasons. The pair at

Table 138. Arctic Skua feeding trips observed during a 24-hour hide watch of a breeding pair at Mucklegrind on 17 July 1976.

Trips by the male			Trips by the female		
Time away	Duration (minutes)	Chicks fed (size in cm.)	Time away	Duration (minutes)	Chicks fed (size in cm.)
0408 - 0447	39	sandeels; 10, 12, 12	0635 - 0710	35	sandeels
0458 - 0528	30		0926 - 1010	44	sandeels
0604 - 0627	23		1308 - 1410	62	
0731 - 0822	51		1631 - 1723	52	
1045 - 1128	43				
1143 - 1226	43	sandeels			
1414 - 1432	18				
1442 - 1529	47	sandeels			
1720 - 1815	55				
1832 - 1908	36				
2114 - 2135	21	sandeels fed to mate			
2135 - 2201	26				

Table 139. Feeding trips by Arctic Skuas observed during a 24-hour hide watch of a breeding pair at the Airstrip on 23 July 1976.

Trips by the male			Trips by the female		
Time away	Duration (minutes)	Chicks fed (size in cm)	Time away	Duration (minutes)	Chicks fed (size in cm)
0454 - 0513	19	sandeels; 10, 10	0400 - 0423	23	sandeels
0517 - 0552	35	sandeels; 5, 5, 8, 8	0752 - 0830	38	sandeels
0602 - 0632	30	sandeels; 8, 8, 8	1029 - 1107	38	
0641 - 0742	61		1400 - 1412	12	sandeels
0847 - 0910	23		1430 - 1445	15	
0911 - 0931	20		1609 - 1613	4	
1108 - 1228	80		2150 - 2210	20	
1229 - 1400	91				
1450 - 1557	67	sandeels			
1622 - 1630	8	sandeels			
1645 - 1702	17	sandeels			
1830 - 1842	12	sandeels			
1921 - 1948	27	sandeels			
2022 - 2103	41	sandeels			

Table 140. Feeding trips by Arctic Skuas observed during a 24-hour hide watch of a breeding pair at Ristie on 24 July 1976.

Trips by the male			Trips by the female		
Time away	Duration (minutes)	Chicks fed (size in cm)	Time away	Duration (minutes)	Chicks fed (size in cm)
0245 - 0400	75	sandeel; 10	0706 - 0835	89	sandeels; 7, 8
0405 - 0704	179	sandeels	1015 - 1048	33	sandeels; 10, 10
0836 - 1008	92		1052 - 1142	50	
1205 - 1352	107	sandeels; 10, 14	1352 - 1435	43	sandeels; 8, 8, 10
1518 - 1806	168	sandeels	1806 - 1854	48	sandeels
1910 - 2018	68		2019 - 2055	36	sandeels

Table 141. Summary of the amount of time spent on and away from the territory by members of three Arctic Skua pairs watched on Foula in 1976, over 24 hour periods

	Time (minutes)/24 hrs.		
	Mucklegrind	Airstrip	Ristie
Both birds together	815	759	452
Only female on territory	432	531	689
Only male on territory	193	150	299
Neither adult on territory	0	0	0

Mucklegrind was watched on 17 July, and was feeding a well grown chick. The pair at the Airstrip, watched on 23 July, were feeding two small chicks, and the pair at Ristie, watched on 24 July, had a well grown chick. Because a small chick is growing rapidly, it requires as much food as a well grown chick. Thus the pair at the Airstrip had the highest daily food requirement. As Arctic Terns and auks disperse from Foula in July, the food available to Arctic Skuas will decline in quantity through this month. This decline is shown by the greater time spent foraging on 24 July by the Ristie pair than was spent on 17 July by the nearby Mucklegrind pair (table 141). In spite of a greater food requirement, the pair at the Airstrip spent less time foraging, and their foraging trips were shorter than those of the Ristie pair watched on the next day. This difference may be due to the greater availability of the species which Arctic Skuas prefer to chase (Arctic Terns and Kittiwakes) near the Airstrip, as predicted to explain the rapid increase in numbers of Arctic Skuas on Foula, and particularly, the concentration around the Arctic Tern colonies adjacent to the Airstrip.

Another consequence of holding territory in a particular part of Foula is that Arctic Skuas in different areas are subject to different territorial conflicts or transgressions. To examine this variation, the three pairs watched were selected from different types of Arctic Skua territories. The Mucklegind pair was in an area of mixed Arctic Skua and Great Skua interspecific territorial boundaries; the Ristie pair was in an area of scattered Arctic Skua territories at the edge of the island, and the Airstrip pair was nesting between sections of the Arctic Tern colony with other Arctic Skua pairs crowded around. The amount of time that each pair had to devote to territorial activities as a result of their particular situation is shown in table 142.

Table 142. A comparison of time spent in flight by Arctic Skuas in their territories in three different types of Arctic Skua breeding habitat on Foula. (Number of occasions disturbed in parentheses). (24 hour watches)

Cause of disturbance	Number of bird-minutes spent in flight / 24 hrs					
	Mucklegrind (Mixed with Great Skua territories)		Airstrip (high density and in tern colony)		Ristie (At edge of island on cliff grassland)	
Great Skua	136	(58)	7	(5)	54	(38)
Arctic Skua	30	(14)	35	(20)	8	(5)
Display flights	59	(14)	21	(5)	17	(5)
Sheep near chick	1	(1)	20	(7)	14	(10)
Arctic Tern	0	(0)	14	(10)	0	(0)
Fulmar	2	(1)	1	(1)	2	(1)
Common Gull	0	(0)	1	(1)	3	(2)
Herring Gull	0	(0)	0	(0)	1	(1)
Great B.-b. Gull	0	(0)	0	(0)	1	(1)
"no reason detected"	6	(11)	1	(3)	1	(2)
Total bird-minutes activity	234		100		101	

Nesting in the vicinity of Great Skuas clearly requires the expenditure of much additional energy, but nesting between tern colonies resulted in little conflict with terns, and only a small amount of time was spent in chasing other Arctic Skuas, in spite of their very high nest density, although intraspecific territorial disputes may well have been important earlier in the breeding season.

Discussion

The Arctic Skua does not seem to influence the Great Skua in any detectable way. Great Skuas affect Arctic Skuas most seriously by increasing adult and fledgling mortality rates and by limiting the space available for Arctic Skua territories, resulting in reduced Arctic Skua breeding success. It is difficult to predict how much further these influences will go. Great Skua numbers in Shetland colonies are not likely to increase much further (section 7), and the habitats now occupied by Arctic Skuas for nesting are ones which Great Skuas may not find acceptable, so further increase may only result in greater Great Skua nest density with little expansion into Arctic Skua habitat. However, it is clear that, in spite of harmful effects on Great Skuas, Arctic Skua colony sizes have varied independently of Great Skua influences.

On Fair Isle, adult Arctic Skuas have an annual survival rate of 0.80 (Davis & O'Donald 1973). Most breed for the first time when four years old (Berry & Davis 1970). Fledgling production varies between colonies, and from year to year, but is usually between 1.0 and 1.3 chicks per pair, so that a first year mortality of about 30% would result in a stable population. Variations in any of these statistics could tend to cause fluctuations in breeding numbers, but the deferred maturity, and variations in age of first breeding between

individuals, would smooth out such fluctuations; it follows that rapid changes in numbers of breeding pairs are likely to be due to high rates of immigration or emigration of recruits. Many seabirds show a tendency to return to their natal area to breed, but this habit may not be well developed in Arctic Skuas, since many individuals ringed as chicks have been retrapped breeding in different colonies (Broad 1973, 1974, British Trust for Ornithology ringing returns) and in Arctic areas this species moves its breeding locality from year to year depending upon the densities of small mammals and Pomarine Skuas (Bertram, Lack & Roberts 1934, Pitelka, Tomich & Treichel 1955). It seems likely therefore, that changes in numbers of Arctic Skuas in Shetland colonies depend little on local effects of Great Skuas, but mainly on the breeding output of all the colonies (which is influenced by Great Skuas at some colonies), coupled with the relative attractiveness of each colony to young, site-seeking recruits. Thus, the rapid increase of Arctic Skua numbers on Foula in the years 1974 to 1976, not paralleled by similar increases at other Shetland colonies, implies that Foula suddenly became more attractive as a breeding site. No clear changes in vegetation, human activity or Great Skua colony area occurred, so this growth is most likely to involve improvements in availability of food.

It is clear that the success rate of Arctic Skua chases varies between victims, being highest with terns and low with auks. Because Kittiwakes carry more fish than auks or terns, they give the highest number of fish per chase, but Arctic Terns make more feeding trips per day than do Kittiwakes or auks (data from Pearson 1964), so that five pairs of Kittiwakes would be required to give as many opportunities for chasing as one pair of Arctic Terns (table 143). Although Arctic Skuas breed successfully in areas where there are few breeding terns

Table 143. Observed chases by Arctic Skuas of seabird species on Foula in 1975 and 1976.

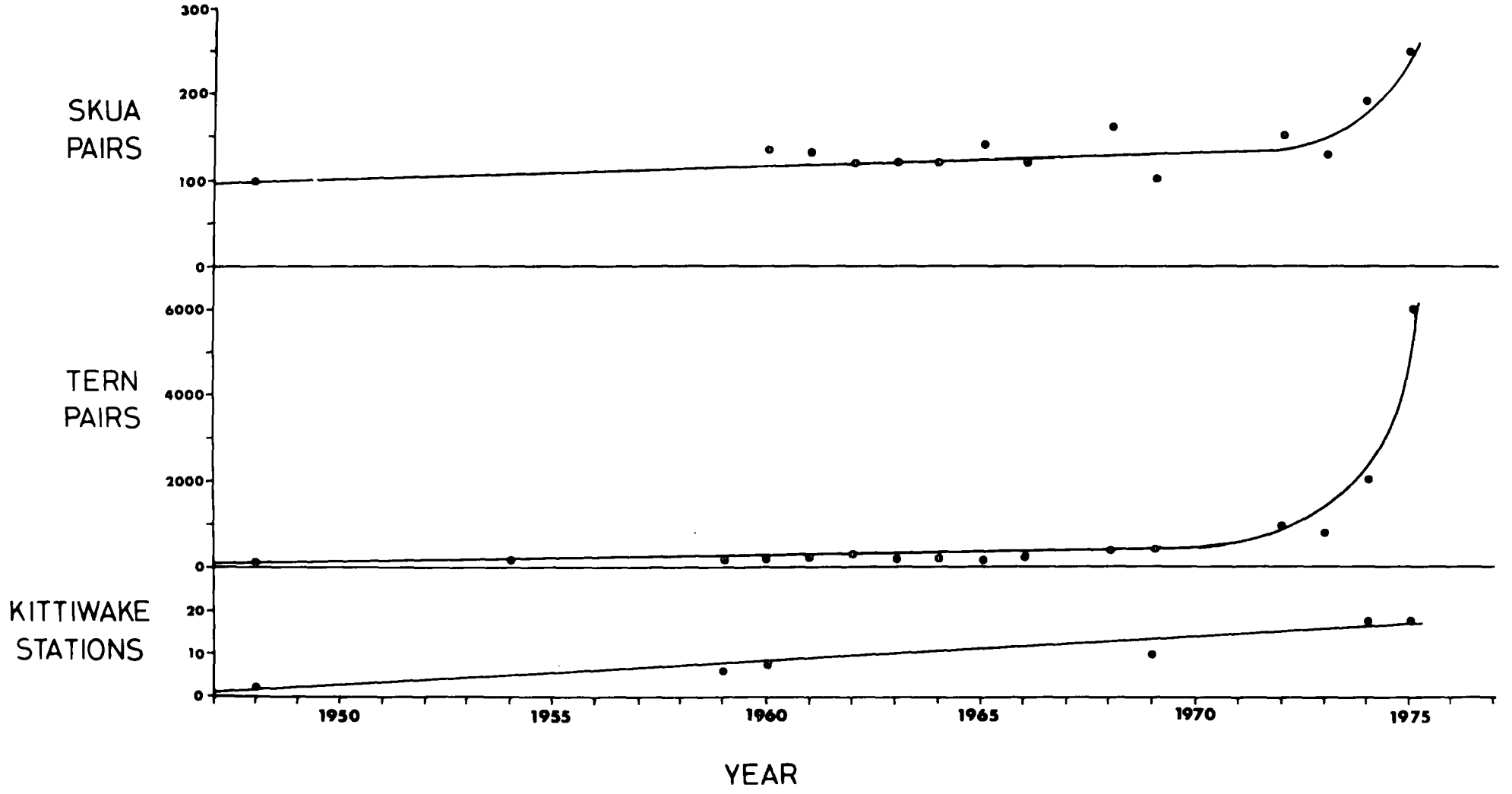
Victim	Number chases observed	% successful	mean number fish obtained per chase	number of feeding trips per day
Arctic Tern	87	43.7	0.44	35
Kittiwake	33	33.3	0.73	7
Puffin	110	20.9	0.37	3
Razorbill	18	11.1	0.11	3
Guillemot	27	11.1	0.11	3

(e.g. Fair Isle), the presence of large numbers of terns might strongly attract recruits to an Arctic Skua population. A similar, but less intense attraction may be provided by large numbers of Kittiwakes, the second most important victims of Arctic Skua chases.

Kittiwake numbers on Foula cannot be adequately counted from the island, and few counts have been attempted from the sea, but the number of Kittiwake breeding stations (Coulson 1963) has increased from one in 1900 to two in 1948 (Pennie 1948), six in 1959 (Coulson 1963), ten in 1969 and 18 in 1975 (Brathay Exploration Group unpublished data), although the most recently formed stations are considerably smaller than the older ones. Arctic Tern numbers have been estimated in many years. Between 1948 and 1970, 12 counts in 12 different years fell between 40 and 400 pairs, with no general trend apparent. Recently, however, numbers have shown a dramatic increase, to 1000 pairs in 1972, 2000 pairs in 1974 and at least 6000 pairs in 1975. In 1975, the terns occupied 0.22 km^2, so were nesting at a density of 0.027 nests m^{-2}, a value similar to the mean density of the same species on Coquet Island (0.02 nests m^{-2}, Langham 1968) but much lower than the highest mean density found on the Farne Islands (2.0 nests m^{-2}, Coulson & Horobin 1976), although this was measured on a vegetation-free area, which allowed higher densities than normal. It is, however, unlikely that the estimated 6000 pairs exceeds the actual number. It is very tempting to explain the changes in numbers of Arctic Skuas on Foula up to 1972 as a slow response to the gradual increase in numbers of Kittiwakes, and the fast increase since 1973 as a response to the influx of Arctic Terns. The closeness of the relationship can be seen in figure 55.

Two principal models of population regulation have been postulated. The simpler states that numbers of breeding pairs result from a balance between the rates of natality and mortality, the latter

Figure 55. Estimates of numbers of breeding pairs of Arctic Skuas, breeding pairs of Arctic Terns, and breeding stations of Kittiwakes during 1948 to 1975 on Foula.


SKUA PAIRS
300
200
100
0
TERN PAIRS
6000
4000
2000
0
KITTIWAKE STATIONS
20
10
0
1950
1955
1960
1965
1970
1975
YEAR

possibly being density-dependent (Lack 1954, 1966). The second states that numbers are intrinsically regulated, possibly by behavioural mechanisms, to a level which does not "overfish" resources (Wynne-Edwards 1962). The breeding success of Arctic Skuas forced to nest at high density, and the increased adult and fledgling mortality, all due to population increases of Great Skuas, would be expected to cause population declines if the first model were acting. If the second model were operative, however, changes in numbers of Arctic Skuas should reflect changes in the availability of food, irrespective of changes in mortality and natality rates (within certain limits). If the effects of Great Skuas are too severe, any behavioural regulation mechanism might not compensate for the increased mortality, but, within the limits, intrinsic regulatory mechanisms would override alteration of mortality or natality. In spite of the reduction in breeding success, and increased adult and fledgling mortality caused by Great Skuas, numbers of Arctic Skuas have increased in many Shetland colonies (Cramp et al. 1974, Sharrock 1976). The magnitude of these changes shows no relation to changes in mortality or production in individual colonies. The colony showing the greatest increase is Foula, where the reduction in Arctic Skua breeding success and increase in mortality due to Great Skuas is higher than in most other Arctic Skua colonies in Shetland. These results are not readily compatible with the first model, but can be explained if Arctic Skua colony sizes are intrinsically regulated through control of recruitment in relation to food availability.

Several studies of bird populations have indicated that there is a surplus of individuals unable to obtain suitable breeding territories (Jenkins, Watson & Miller 1963, Krebs 1971, Watson & Moss 1970). This may apply to the Arctic Skua in Shetland, as non-breeders gather

in "clubs" around the colony, until they are able to estiblish a territory. Young (1972) found that removal of an individual breeding McCormick's Skua from its territory was followed within 48 hours by its replacement by a bird from the club, which then bred in that territory. Arctic Skuas in Shetland do not normally breed until three to six years old (Berry & Davis 1970), although in arctic Russia there are indications that they may do so when only one or two years old (Belopolskii 1961). This suggests that the deferred maturity in Shetland is probably a social rather than a physiological limitation. The mechanism involved is unknown, although dominance hierarchies are found among club members in skua colonies (Perdeck 1960, 1963) and could act to suppress hormonal development of subordinate members (Wynne-Edwards 1962). Breeding skuas are thought to take part in club displays (Perry 1948, Young 1963); their reasons for doing so are unknown, but if their behaviour is modified by food availability, this could provide a mechanism for colony size regulation.

If, as suggested, Arctic Skua colony sizes are intrinsically regulated in relation to local food abundance, current increases should theoretically be following increases in numbers of the main prey species. This has already been shown to be the case for the colony in Foula. Kittiwakes are increasing in most areas in Britain (Coulson 1963, Cramp et al, 1974), while Arctic Tern numbers are known to fluctuate greatly from year to year, with occasional movements of whole colonies to new sites (e.g. Venables & Venables 1955). Recent changes in tern populations in Britain have been documented by Lloyd, Bibby and Everett (1975) and suggest a general decline in Arctic Tern numbers. The national trend is not followed in Shetland: all the colonies have shown increases since 1969, the most pronounced being on Foula, Yell and Skerries (annual Shetland Bird Reports). These

increases may be due to a redistribution of the huge Westray and Papa Westray colonies in Orkney, which have declined in size by an estimated 10,000 pairs since 1969. It could be predicted that Arctic Skua numbers in Shetland colonies will show a consistent relationship with the numbers of Arctic Terns and Kittiwakes, terns having a much more important influence, but at present census data for Shetland are not sufficiently precise to allow this prediction to be tested. Enlargement of Great Skua colonies may have some further effect on the distribution of Arctic Skuas, but is unlikely to continue for many more years. Consequently, the interactions between the two species will probably not be harmful to the populations of either.

SECTION 7

POPULATION DYNAMICS

Adult survival rate

From the results of monel ringing of Great Skuas on Foula, which has continued since 1963, the adult survival rate can be estimated. For many species of bird it has been shown that there is very little variation in the survival rates of age groups more than one year old, while birds less than one year old have lower survival rates. Although it has recently been shown for one long lived seabird that adult mortality rate increases slightly with age (Coulson & Wooller 1976), it is convenient, and necessary with the limited data available, to assume the survival rate of all birds more than five months old (in other words at least one calendar year after the year of hatching) to be constant. Using the method of Haldane (1955) for incomplete recovery data, the survival rate of birds aged more than five months can be calculated, but this calculation assumes that deaths of all age groups are equally likely to be reported. This is clearly not the case, as young Great Skuas suffer greater mortality due to shooting and catching, both of which are more likely to be reported than deaths due to other causes. The differences in the geographical distribution of different age groups also suggests that biases are likely to arise; in particular, many recoveries occur at the breeding colony, which is not visited by one and two year old birds. Clearly the recovery data are heterogeneous, and this is likely to result in a seriously biased survival estimate if Haldane's method is applied uncritically.

An alternative approach is to examine the relationship between the $\log_{10}$ (proportion of available birds recovered of age i) against the age in calendar years from hatching (i). The slope of this line, if not subject to biases in chances of recovery of different age groups, gives the adult survival rate (recoveries of birds before the end of the calendar year in which they hatched are excluded from calculations of slope). Visual inspection of the plot of $\log_{10}$ recovery rates against age, when all recoveries are included, shows that birds under three years of age fall well below a regression equation based on older ages only (figure 56), indicating their pelagic nature and wide dispersal at these times (as shown earlier), which results in fewer deaths being reported than for older birds. When only those birds recovered at Foula during the breeding season are included in a plot against age, it becomes clear that recoveries at the breeding colony can only be used to estimate the survival rate of birds more than four years old (figure 56). At younger ages the recovery rates do not represent mortality rates as many birds are not present at the colony. Recovery rates of birds more than four years old show a constant rate of decline, the slope of which is the survival rate.

It can be hoped that by excluding recoveries of birds in breeding areas during the summer, the recoveries of individuals reported as killed, found exhausted or caught in nets or on lines, and plotting recovery rates of birds found dead outside the breeding season against calendar year of age, the biases mentioned above would be minimised. Unfortunately these exclusions severely reduce the number of recoveries available for the analysis, but the relationship appears to be linear for all ages between one and 14 calendar years after hatching (figure 56). Survival rates for these three categories of recovery are given

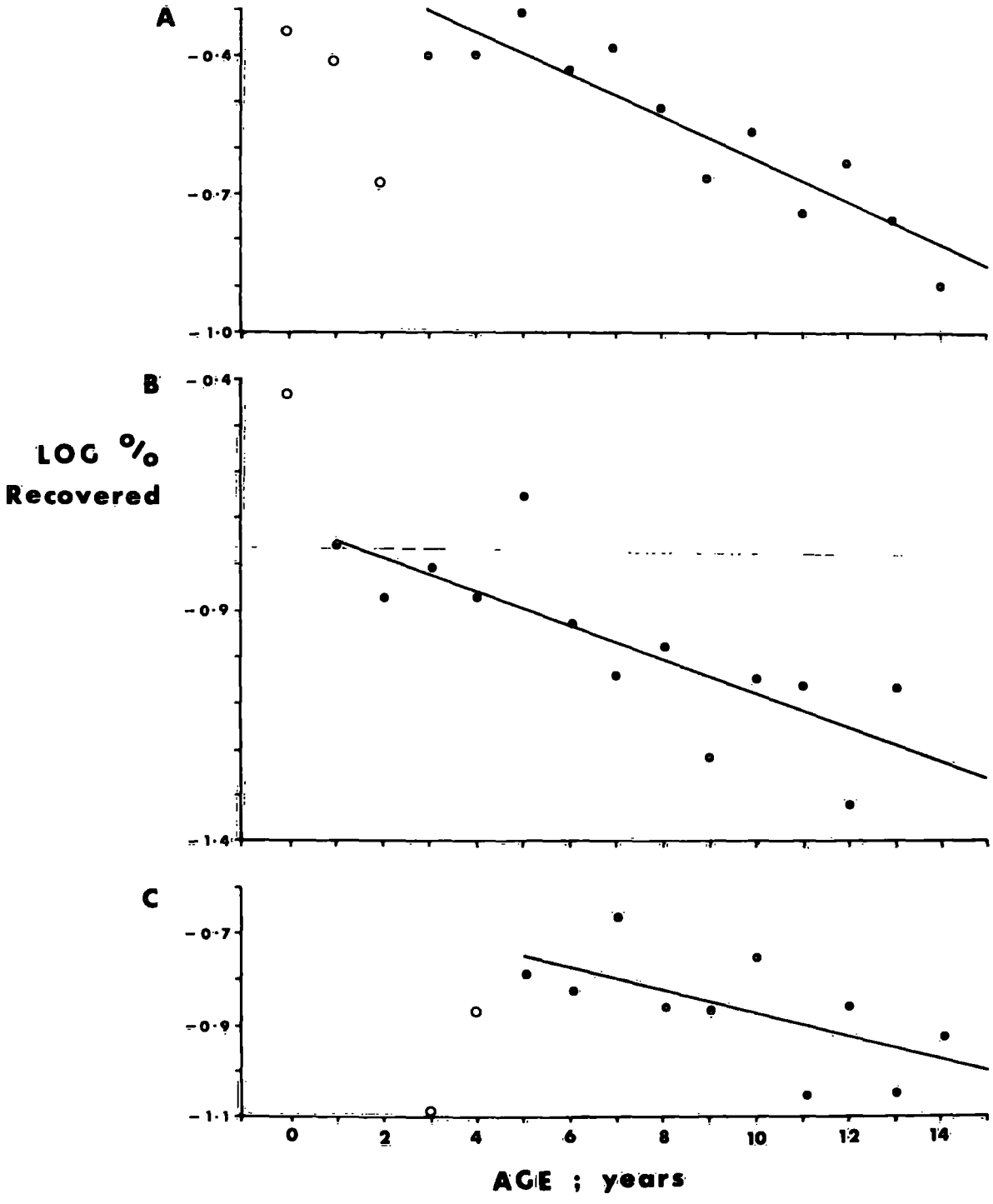
Figure 56. Recovery rates of Great Skuas of each year of age. Log_{10} (% recovered) is plotted against age in calendar years after ringing for:

a) all recoveries of Great Skuas ringed at Foula

b) only those reported as found dead not on Foula

c) only those recovered on Foula

Points which are influenced by one of the biases listed in the text are marked (o). Regressions used to estimate adult survival rate are shown, and the points on which the regressions were calculated are marked • . The antilog of the slope is the adult survival rate.


A
B
C
-0·4
-0·7
-1·0
-0·4
-0·9
-1·4
-0·7
-0·9
-1·1
0
2
4
6
8
10
12
14
LOG %
Recovered
AGE ; years

in table 144. For comparison the survival rates obtained using Haldane's method for each of these limited categories of recovery data are also tabulated.

In 1975, 1976 and 1977, the numbers of ringed adult Great Skuas found dead on Foula were greater than in earlier years because I was present on the island to find corpses for long periods of time, in addition to the time spent by Brathay expeditions. As a result, there were disproportionately high numbers of recoveries of all age classes in these seasons. Haldane's method for incomplete recovery data requires the probability of recovery to remain constant through the period of study, and thus gives a biased estimate of the survival rate when used with the recoveries from Foula. The regression technique does not make this assumption. For these Great Skua recovery data, the best estimates of the survival rate of adults are therefore the regression estimates for Foula recoveries, and for "found dead not on Foula" recoveries (figure 55, table 144). These are independent estimates of $\underline{s}$, so can be combined to give an estimate of the survival rate ($\underline{s}$) of 0.93 (se = 0.02), based on 236 ringing recoveries. From this estimate the further expectation of life of a Great Skua reaching breeding age can be estimated to be $(2 - m) / 2m$, where $\underline{m}$ is the mortality rate $(1 - s)$, giving expectation of 13.8 years, with 95% confidence limits of 8.6 years and 32.8 years.

Mortality rates of fledglings and first year birds

Compared with adults, Great Skuas in their first year of life suffer higher mortality rates due to shooting, exhaustion and being caught in nets and on lines. Their survival rate will be lower than that of adults. However, the chances of a ringed bird being reported to the BTO are presumably much higher for birds killed or caught than

Table 144. Survival rates of adult Great Skuas from Foula obtained from analyses of ringing recovery data.

Data used	Ages included	number of recoveries	method used	estimated survival rate	95% confidence limits
All recoveries	3 - 14 years	283	regression	0.899	0.868 - 0.931
			Haldane's	0.919	
Foula recoveries only	5 - 14 years	81	regression	0.944	0.888 - 1.000
			Haldane's	1.190	
Found dead, not on Foula only	1 - 14 years	155	regression	0.918	0.875 - 0.961
			Haldane's	0.905	
Foula only combined with found dead not on Foula only		236	regressions	0.93	0.89 - 0.97

for birds recorded as "found dead", so this greater mortality rate is likely to be greatly exaggerated by an analysis which includes all recoveries.

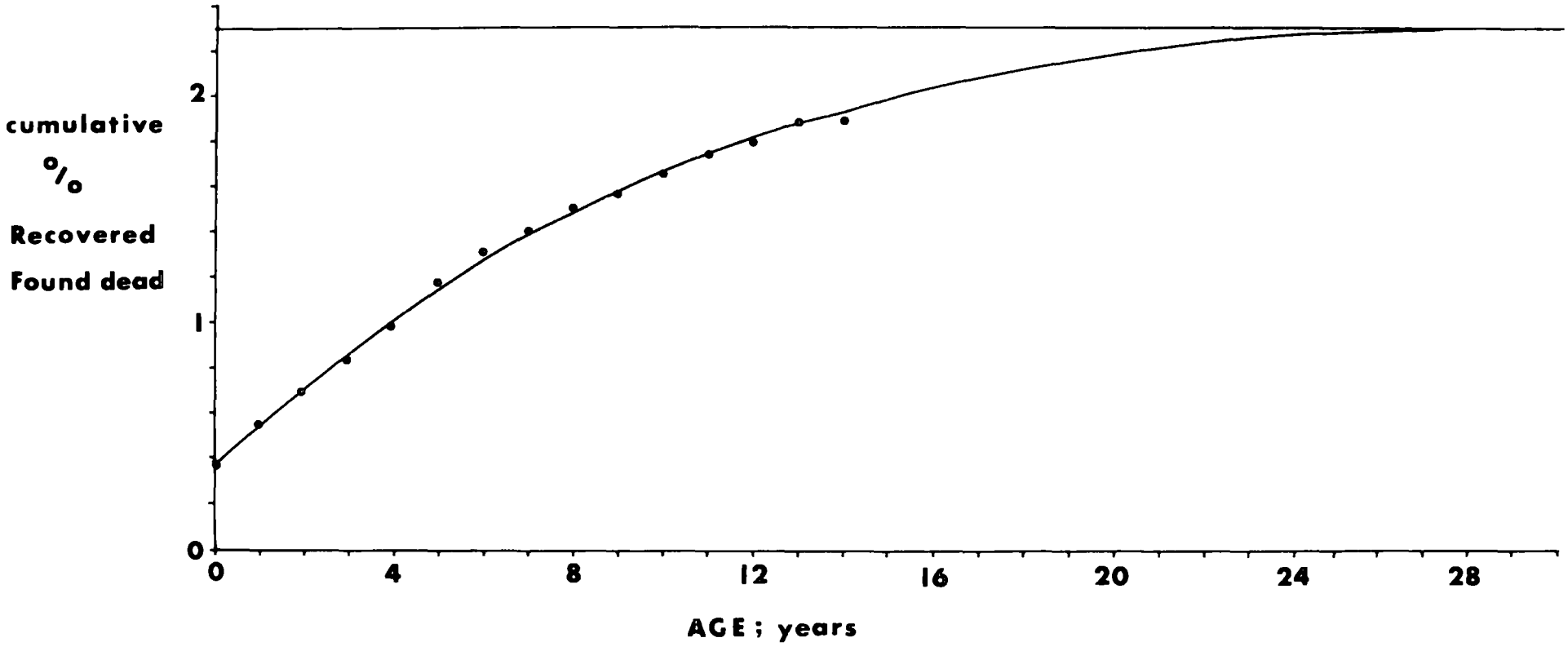
Even first year birds "found dead" are likely to be biased when compared with adult recoveries, as first year birds are likely to die in unusual places, where their chances of being found and reported are higher, while adults are more likely to die at sea so not be recovered. Such a bias was shown in the ring recovery data for the Shag (Potts 1969).

The percentage of ringed birds which will have been reported as found dead when the entire cohort has died can be estimated by extrapolating to an asymptote through the cumulative percentages of birds recovered "found dead" in successive cohorts. This (figure 57) estimates that 2.3% of all chicks ringed with monel rings will eventually be reported as found dead. Between fledging and the end of the first calendar year (6 months old) 0.373 % of ringed chicks are found dead. In the next complete calendar year (up to 18 months old) another 0.173 % are found dead. These represent 24 % of the final total found dead, suggesting mortality rates of 16% in the first six months, 20% in the first 12 months and 24% up to the end of the second calendar year (18 months). With the probably tendency for too many first year birds to be found, these are more likely to overestimate the mortality rates in the first 18 months of life than to underestimate them.

Compatibility of estimated population parameters

Capildeo & Haldane (1954) have produced tables from which rates of population increase can be calculated given values of adult survival

Figure 57. Curve to estimate the percentage of ringed Great Skuas which will be reported as found dead when all individuals have died. This value is the asymptote of the plot of cumulative percentages of ringed Great Skuas reported as found dead, against the age of the bird when recovered, in calendar years. From this figure the final percentage recovered as "found dead" is estimated to be 2.3 %.


cumulative
%
Recovered
Found dead
2
1
0
0
4
8
12
16
20
24
28
AGE ; years

rate, age of first breeding and net fertility.

Very few colour ringed birds bred before they were six years old. Most five and six year old birds left club sites to establish territories, but would not breed until the next year, and a small number of club birds were at least eight years old but had not established a territory. Thus the mean age of first breeding must be at least seven years old, and probably no more than eight years old. We now also have estimates of adult survival rate, chick production per pair and first year survival rate for Foula Great Skuas. Net fertility is defined as the number of female progeny alive at the time of laying in the next year, per breeding adult female, calculated by;

$$f = ck / 2s \qquad \text{(Capildeo \& Haldane 1954)}$$

where $\underline{c}$ is the mean clutch size, $\underline{s}$ is the adult survival rate and k is the proportion of eggs producing chicks which survive to one year of age. For Foula Great Skuas net fertility is therefore;

$$\frac{\text{(mean clutch size) x (breeding success) x (survival rate in first 12 months)}}{\text{2 x (adult survival rate)}}$$

or (1.894)(0.653)(0.80) / 2(0.93) which equals 0.532. If it is assumed that the mean age of first breeding is eight years, then, from their tables, the rate of increase of the Foula Great Skua colony should be 8.9 % per annum. In fact it has remained constant since 1900 at 7.00 % per annum (appendix 2), suggesting that the breeding success or survival rates may have been slightly overestimated, the age of first breeding underestimated, or there may be net emigration of birds from the Foula colony to other areas. The two study years were of

better than usual food availability, so breeding success is probably lower when averaged over a large number of years, and the survival estimates are not very precise, so the agreement achieved is satisfactory.

Rates of increase in different colonies

Between 1900 and 1976, the Great Skua has bred in 32 distinct areas in Britain. In seven of these breeding did not continue, or numbers failed to increase after the initial colonisation. Six areas have been colonised so recently that the growth trends in these areas cannot yet be determined. In one area, Yell, the numbers of breeding pairs failed to increase at first, then increased extremely rapidly, then the rate of increase fell quickly towards zero. In all other areas numbers have increased exponentially for most or all of the period of colony existence since 1900. Ten colonies have increased at a constant rate, one shows evidence of an initial influx of some six to ten pairs followed by a constant rate of increase, three initially increased at a constant rate then the rate decreased towards zero, and four showed a delay after the initial colonisation before assuming a constant rate of increase. However, the rate of increase varies greatly between colonies (table 145).

By summing counts at each colony, or logarithmic interpolations between counts for 1900, 1910, 1920, 1930, 1940, 1950, 1960, 1970 and 1975, the rates of increase of the entire British population (considered to be a closed population) can be determined over these intervals. In the first four decades the rate of increase averaged 7.2% per annum, compared with only 6.0% per annum over the last four periods. The difference is significant (Mann-Whitney $U = 16$, $p = 0.05$), indicating

Table 145. Rates of increase of British Great Skua colonies between 1970 and 1976, and during the phase of constant rate of increase (exponential growth), together with the order of colony establishment and the rank of colony size (rank of 1 is the largest colony) in 1976. Values in parentheses are based on few data points. Rate of increase at Fair Isle was calculated only for periods when no shooting of Great Skuas was carried out.

Pattern of colony growth.	Colony	Order of establishment	Rank of colony size in 1976	Rate of increase during phase of constant rate	Period of constant growth rate	Rate of increase between 1970 and 1976
Constant rate of increase	St. Kilda	17	15	(25.9%)	1962 - 1976	(25.9%)
	Fair Isle	11	12	22.2% 22.2%	1945 - 1958 1970 - 1976	22.2%
	Handa	19	17	(21.2%)	1964 - 1976	(21.2%)
	Hoy	10	3	10.8%	1914 - 1976	10.8%
	Lewis	14	14	9.5%	1945 - 1976	9.5%
	Rousay	16	18	9.1%	1955 - 1976	9.1%
	Bressay	9	9	8.7%	1913 - 1976	8.7%
	Vaila	15	16	8.4%	1948 - 1976	8.4%
	Foula	1	1	7.0%	1900 - 1976	7.0%
	North Rona	18	19	5.8%	1964 - 1976	5.8%

Table 145. Rates of increase of British Great Skua colonies between 1970 and 1976, etc. - Continued.

Pattern of colony growth	Colony	Order of establishment	Rank of colony size in 1976	Rate of increase during phase of constant rate	Period of constant growth rate	Rate of increase between 1970 and 1976
Influx then a constant rate of increase	Hermaness	2	2	4.9%	1900 - 1976	4.9%
Constant rate then falling rate towards zero	Noss	7	6	15.5%	1910 - 1932	0.0%
	Hascosay	8	10	15.0%	1912 - 1925	0.0%
	Saxavord	4	4	12.6%	1890 - 1910	2.9%
Delay after initial colonisation then constant rate of increase	Fitful Head	12	11	10.6%	1950 - 1976	10.6%
	Mainland north	3	8	9.6%	1930 - 1976	9.6%
	Fetlar	6	7	9.6%	1920 - 1976	9.6%
	Mousa	13	13	8.0%	1955 - 1976	8.0%
No constant rate	Yell	5	5	no constant rate		2.5%

that the rate of increase is falling as numbers, and population density, increase.

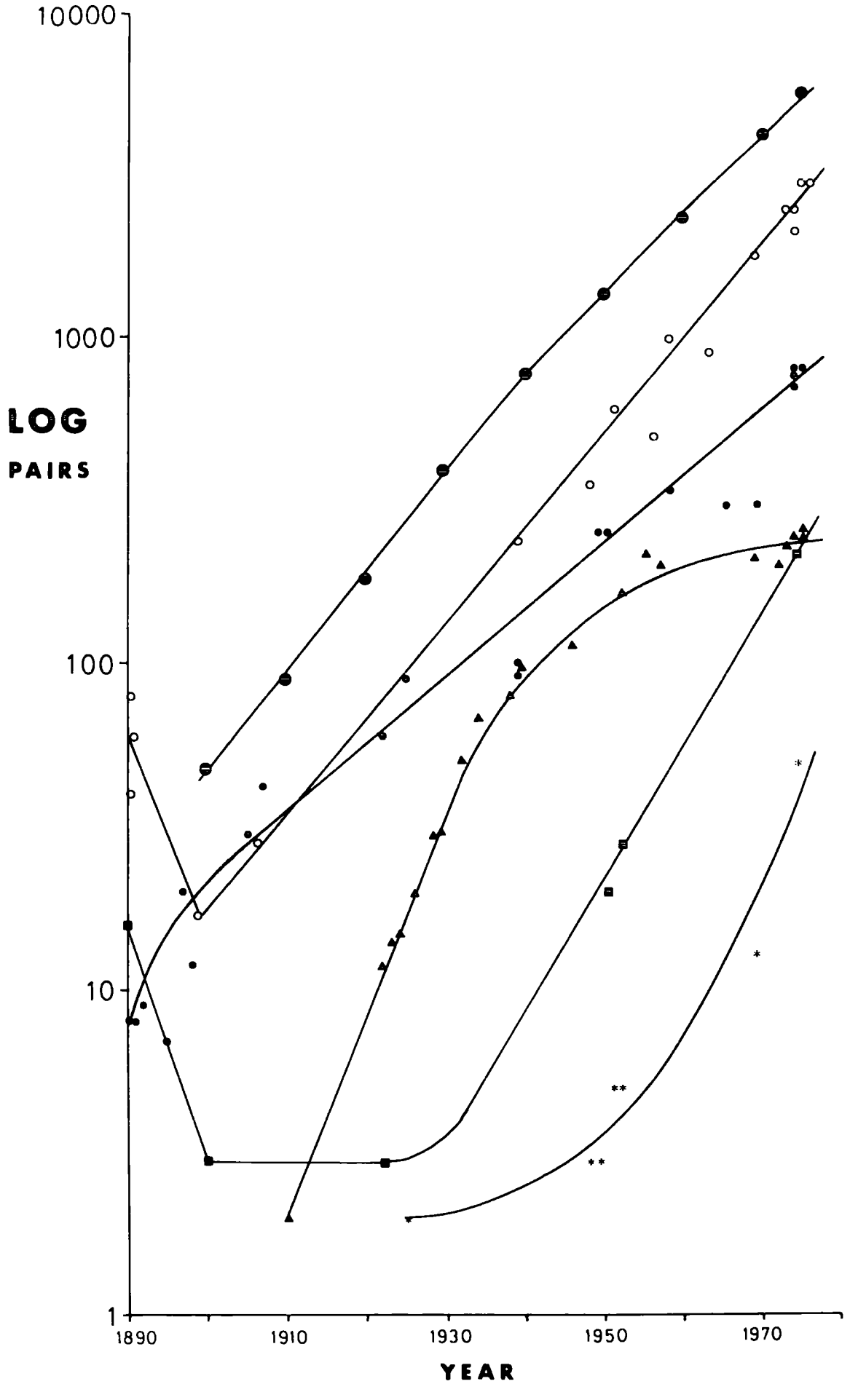
This curve, and representative curves of the types described above, are shown in figure 58.

Of the 26 areas where trends are clear, none of the first 13 to be established failed to grow into colonies, whereas seven of the more recently formed 13 have failed to become established. This suggests that there are few areas left in Britain which would support a Great Skua colony but have not yet been colonised, but it is not clear what the limitations of uncolonised areas are. In this context it is noteworthy that Great Skuas colonised Bear Island in 1969 (Munkebye 1973) and Norway in 1975 (Vader in litt.); these are likely to be extensions of the British population, as numbers of recoveries of three to five year old British Great Skuas have been increasing in these areas in recent years.

It is not at all clear why the rates of increase should be consistent within colonies but very variable between colonies. There is a very close correlation between the order of colony establishment and ranked colony size in 1976 (1 is the biggest colony) ($r = +0.916$, $df = 17$, $p < 0.001$), in spite of the variations in colony growth rates, but there is also a tendency for recently established colonies to have the highest growth rates ($r = +0.526$, $df = 17$, $p < 0.05$). No comparative data are available to determine whether rates might depend on differences between colonies in breeding success or adult survival, but the highest rates of increase must be due to net immigration, so presumably low rates are likely to be due largely to net emigration. This implies that colonies vary in attractiveness to recruits. There are a few records of individuals breeding in colonies other than their natal one. Some 20 colour ringed individuals (ringed as chicks on

Figure 58. Rates of increase of different colonies of Great Skuas during the period 1890 to 1976. The $\log_{10}$(number of breeding pairs) is plotted against the year of the count, so the slope of each curve gives the rate of increase. Colonies are:

- ⊜ Total British population
- o Foula
- ● Hermaness
- ■ Shetland mainland
- ▲ Noss
- * Fitful Head


10000
1000
100
10
1
LOG
PAIRS
1890
1910
1930
1950
1970
YEAR

Foula) have been found breeding on Noss, Hermaness, Saxavord and North Rona. Nearly one quarter of recruits to Fair Isle were ringed as chicks on Foula, implying that about half the Fair Isle Great Skua population emigrated to there from Foula.

The three colonies which have almost reached asymptotes were colonies with very high rates of increase, and all three occupy relatively small breeding areas, but nest density per se does not appear to be a limiting factor. Foula has a higher nest density than any other colony, but is still increasing at a constant rate of 7.0% per annum, which is now higher than the rate of increase of the total British population, but Hermaness, where nest density has not increased above the 55 nests km^{-2} found in 1922, is only increasing at 4.9% per annum.

SECTION 8

DISCUSSION

The breeding biologies of many species of seabird have been studied in detail, and the results of this study show that the Great Skua fits into the pattern shown by other skuas and large gulls. The areas where the Great Skua differs from other species are of the greatest interest. The history of the Great Skua populations in the North Atlantic are very different from any other species. It is the most recent colonist of the North Atlantic seabird communities, and the British and Faroe populations have passed through more severe bottlenecks than suffered by any other seabirds in the North Atlantic. This appears to have caused inbreeding depression (infertility) in the British population, a phenomenon which has not been shown in any other wild avian population, although further studies are required to rule out influences of PCB and mercury.

Although gulls, Gannets and other seabirds have clubs used by prebreeders, no other seabird has been shown to have club sites which are traditional in their location, and around which poor quality individuals nest in small territories. Segregation of birds in colonies into "good" and "bad" areas has been shown in the Kittiwake, where birds in the centre and on the edge of a colony differ in quality (Coulson 1968), but the social structure of the Great Skua colony, with poor quality pairs confined to small areas of high nesting density, appears to be unique.

Belopolskii (1961) showed that the diets of male and female Arctic Skuas and large gulls tended to indicate that males forage at sea and females forage to a large extent close to the nesting area.

This dimorphism is taken one step further by the Great Skua which, in Shetland, divides foraging and nest protection between the sexes. The female obtains most of her food from her mate throughout the nesting period. This is similar to the situation with large birds of prey, but contrasts with most seabirds, which tend to share in foraging.

As there do not seem to be many areas in northern Britain which could support a new Great Skua colony, it would appear that the species will increase in the future mainly by growth of present colonies or extension of range. Some colonies for example St. Kilda and Hoy, have considerable room for spread, but most can now only increase in numbers by increase in nest density. With the tendency for breeding success to fall at higher nest densities a limit could eventually be reached. Low or variable food availability would cause this limit to occur at lower nest density.

Although Great Skuas at Foula feed mainly on sandeels, fishing boat reject fish forms an important part of their diet. Presumably the temporary absence of sandeel shoals is less harmful to Great Skua breeding success if the birds can turn to fishing boats as an alternative food source. The lack of this alternative would mean that sandeel scarcity would force Great Skuas to spend many hours in kleptoparasitism, scavenging and predation, all of which appear to be time consuming and relatively unrewarding activities. As a result, high rates of nest predation would be expected. Thus gleaning fish from fishing boats probably allows Great Skuas to nest at higher densities than would be the case if undersized and unwanted species of fish were not rejected by fishing boats as at present. Any change in the current whitefish fishing pattern or catch regulations could have a very pronounced effect on Great Skua breeding success in some seasons, while other seabirds such as Fulmars and Larus gulls would

probably be less seriously affected, and auks, terns, petrels, shearwaters, Shags and Kittiwakes probably not affected at all except perhaps by increased Great Skua predation and kleptoparasitism.

The current upsurge of industrial fishing around northern Britain for sandeels and Norway Pout may provide Great Skuas with some refuse and spillage of fish, but the long term effect of intensive fishing on sandeels may be to reduce the food availability for both whitefish and seabirds. Although the growth rate of sandeels is very rapid, so that fishing in one season will have little effect on sandeel biomasses in subsequent seasons, heavy industrial fishing around seabird colonies in the early summer could disrupt and disperse sandeel shoals and cause a large reduction in the biomass of sandeels for the rest of that season (until the next generation is recruited). The effect on all seabirds would be to drastically reduce the food availability. This would most seriously affect species with short feeding ranges and a high dependency on sandeels, such as Arctic Terns and Guillemots, but would also force Great Skuas to depend on fishing boat reject fish, and fluctuations in the availability of these, which might also be expected to occur as a result of the failure of whitefish to find sandeel shoals, would be expected to result in high rates of egg predation, so that breeding success would fall below the level required to maintain the population increase.

Bans on Haddock and Whiting fishing around Shetland or intense sandeel fishing in inshore areas could both result in Great Skua breeding failures, particularly at colonies like Foula or Noss, where nesting densities are high. Both of these appear to be likely to occur in the next decade unless the EEC fisheries policy is altered.

SUMMARY

This study adds to the small literature on the North Atlantic Great Skua, through an examination of aspects of Great Skua breeding biology and population changes, particularly in northern Britain.

1. Six colony census techniques for the determination of numbers of breeding pairs of Great Skuas are evaluated. The currently recommended method of counting aggressive territory owners is shown to give estimates biased 25% below the true number of pairs and with a 95% confidence interval of ± 25%, in spite of large numbers of people and time required to carry out. Direct counts of territories give a 10% underestimate of numbers but require no more than a few days for one person to complete, so are to be preferred.

2. It seems probable that the Great Skua colonised Iceland between the 12th and 15th centuries, then spread to Faroe, only colonising Britain in the 1760's. Numbers of pairs seem to have changed little in Iceland in recent years, but both Britain and Faroe populations suffered periods of persecution before 1900, after which rapid increases have occurred. Counts at each British and Faroe colony are tabulated in detail.

3. Aluminium rings fall off or are pulled off by Great Skuas after two to five years of wear. Monel rings, used since 1963 on Foula, suffer no detectable wear. Proportions of recoveries reported as killed, caught, exhausted or found dead vary geographically, and differ between age classes. Young birds are more susceptible to "wrecks", which can be demonstrated to have occurred in the autumns of 1939, 1963 and 1969. Since 1966 the recovery rate of first year birds has fallen significantly and recoveries in the North Sea now form a smaller proportion of the total, suggesting the evolution of a more pelagic dispersal.

Variations in recovery rates of second year and third year

birds are significantly correlated with recovery rates of first year birds, indicating that years of bad weather affect all age groups. Recovery rates of cohorts in successive seasons are also significantly and positively correlated, indicating that birds may be unable to completely recover from effects of bad weather in one autumn before the next autumn.

First year birds move to southern Europe in the winter, with most recoveries on the coast of Spain and Portugal. In summers before the fifth year some birds visit high latitudes between Greenland and Spitzbergen. Winter movements become shorter with many birds remaining in British waters when more than 5 years old.

Prebreeders, some marked with colour rings, return to breeding colonies and gather on traditional club sites. Younger prebreeders return later than older prebreeders. Few two year olds visit breeding colonies but most four year olds spend most of the breeding season at the colony.

Breeders first return to the colony at the end of March, making short visits onto the island at midday. Visits quickly extend in duration as territories are reoccupied. The greeting ceremony is particularly frequent at this time and may result in social stimualtion and coordination over small areas of the colony.

4. The use of models to study energy requirements of avian populations or communities is reviewed. An improved model is presented which can be used to calculate energy requirements of seabird populations. The sensitivity of the model to errors in input parameter values is examined and a Monte Carlo technique is employed to estimate confidence intervals for output energy requirements.

Composition of the Great Skua diet was examined by collecting regurgitated pellets, recording bird corpses attributed to Great Skua

predation, and examining food regurgitated by chicks. Sandeels were the largest single component of the diet, forming a higher proportion of the chick diet than the breeders' and a lower proportion of the prebreeders' diet. Diet composition varied seasonally and between years, and time budgets indicated that the periods when sandeels formed only a small part of the diet were periods of food shortage, requiring long foraging trips. It was inferred that direct fishing on sandeels is the main preferred feeding method, fishing boats provide an alternative food source when sandeel shoals are not available, scavenging, predation and kleptoparasitism are minor feeding methods, used mainly when there is difficulty in obtaining food by the preferred means.

Food specialisations exist within and between colonies; predation by nonbreeders occurs mainly at sea, and breeding females may specialise on prey close to their territory. A large proportion of birds in the Great Skuas' diet are probably eaten as carrion. No bird population on Foula appears to be declining as a result of Great Skua predation.

5. A discriminant function was calculated which correctly classifies 94% of eggs into first or second laid. No egg parameter was found to show a consistent relationship with parent age or experience, but egg length and breadth tended to decline seasonally. A discriminant function was calculated to determine chick ages in the first five days after hatching; 99% were classified to within one day of their correct age.

Late hatched chicks show reduced weight gain but very little reduction in wing or leg growth rates when compared to earlier hatched chicks. Weight deviations are greatest for second hatched chicks in

broods of two and most pronounced between 9 and 39 days after hatching. Growth rates of chicks hatched before 20 June in 1975 were homogeneous and were defined as "typical" growth. Conversion tables to give age from chick measurements were calculated.

Cadmium levels in Great Skuas are very high, but probably harmless. Levels of mercury and PCB's are high and may be impairing breeding success. DDE and Dieldrin levels are fairly low and no eggshell thinning is detectable. Abnormally high rates of embryo mortality and chick deformity appear to be due to PCB and mercury. While high rates of egg infertility might be due to mercury, they might be due to inbreeding and low rates of natural selection in the British population, which appears to be genetically isolated from the Iceland and Faroe populations.

Experienced pairs arrive at the colony earlier than inexperienced pairs, lay earlier, and fewer of their chicks starve to death. Nest density does not influence laying dates, but breeding success is lower at higher nest densities because egg predation is more frequent. Less aggressive pairs are more susceptible to egg predation but aggression indices do not vary in relation to nest density in non-club areas. Food shortage appears to increase rates of egg predation, particularly at high nest densities. Poor quality pairs are forced to nest in club territories, at very high nest densities, because nesting space is limiting on Foula. These pairs lay late, have low aggression indices and low breeding success.

Second laid eggs have the same hatching success as first laid, but more second hatched chicks starve to death as a result of asynchronous hatching. Clutches of one egg, which comprise 10% of all clutches, suffer higher predation, infertility and chick starvation, pointing to low quality of pairs laying single eggs.

Egg predation and addled eggs cause 74% of egg and chick losses. Breeding success in the two seasons averaged 65%, or 1·24 fledglings per breeding pair.

6. Claims that Great Skuas have caused many other species to decline in numbers are inconsistent with census data, but the Arctic Skua does appear to be a potential competitor. This species has also increased in numbers in Shetland. Arctic Skuas on Foula suffered predation of 4% of adults and 21% of fledglings each year by Great Skuas. These represent a negligible part of the Great Skuas energy requirements but a large reduction of Arctic Skua survival rates. Arctic Skuas feed mainly by kleptoparasitism, a technique little used by Great Skuas. Methods of kleptoparasitism are different, and there is very little overlap in species chased by each skua. At Foula, Arctic Skuas mainly rob Arctic Terns, Kittiwakes and Puffins, while Great Skuas mainly rob Guillemots, Razorbills, Puffins and Gannets. Chases of the preferred victims have the highest success rates. Factors influencing probability of success vary more between types of victims than between skua species. Auks tend to avoid skuas by diving into the sea, and speed of reaction to an approaching skua is the main determinant of success. Gulls and terns are best robbed by persistent harrying. Speed and manoevreability are the Arctic Skuas main assets while surprise diving attacks are the Great Skuas main technique. Speed of reaction was influenced by local visibility while method of evasion depended largely on the height of the victim above the sea.

Competition for territories has resulted in Arctic Skuas being pushed into suboptimal habitats by the increasing Great Skua. Nest densities have increased as all suitable habitat becomes occupied, and breeding success has decreased as a result. Arctic Skua numbers

on Foula have shown a close relationship with numbers of Arctic Terns, suggesting that a nonbreeding reserve exists which is currently buffering the harmful effects of Great Skuas. As a result it seems unlikely that interactions will be harmful to either skua species.

7. Ring recovery data are heterogeneous, but adult survival rates can be estimated from recoveries of birds aged 5 to 14 years, on Foula, and independently from recoveries of birds aged 1 to 14 years reported as found dead outside breeding areas. The survival rate of adults is estimated to be 0·93, and the survival rate of birds in their first year is estimated to be 0·80. Rates of increase vary between colonies but agree well with the rate predicted from estimates of survival rates, age at first breeding and fecundity. The rate of increase of the British population is falling as the population grows.

8. Changes in patterns of whitefish fishing or increases in industrial fishing around Great Skua colonies could drastically reduce breeding success of Great Skua colonies. Such changes appear to be likely to occur.

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APPENDIX 1. Latin names of species mentioned in the text.

BIRDS

Red-throated Diver	Gavia stellata (Pontopp.)
Great Northern Diver	Gavia immer (Brünn.)
Slavonian Grebe	Podiceps auritus (L.)
Fulmar	Fulmarus glacialis (L.)
Sooty Shearwater	Puffinus griseus (Gm.)
Audubon's Shearwater	Puffinus l'herminieri (Lesson)
Manx Shearwater	Puffinus puffinus (Brünn.)
Storm Petrel	Hydrobates pelagicus (L.)
Leach's Petrel	Oceanodroma leucorrhoa (Vieill.)
Brown Pelican	Pelecanus occidentalis (L.)
Gannet	Sula bassana (L.)
Cormorant	Phalacrocorax carbo (L.)
Shag	Phalacrocorax aristotelis (L.)
Grey Heron	Ardea cinerea (L.)
Grey-lag Goose	Anser anser (L.)
Shelduck	Tadorna tadorna (L.)
Mallard	Anas platyrhynchos (L.)
Teal	Anas crecca (L.)
Wigeon	Anas penelope (L.)
Scaup	Aythya marila (L.)
Eider	Somateria mollissima (L.)
Common Scoter	Melanitta nigra (L.)
Long-tailed Duck	Clangula hyemalis (L.)
Red-breasted Merganser	Mergus serrator (L.)
Sea Eagle	Haliaetus albicilla (L.)
Pheasant	Phasanus colchicus (L.)
Coot	Fulica atra (L.)
Oystercatcher	Haematopus ostralegus (Neumann)
Ringed Plover	Charadrius hiaticula (L.)
Golden Plover	Pluvialis apricaria (L.)
Lapwing	Vanellus vanellus (L.)
Turnstone	Arenaria interpres (L.)
Dunlin	Calidris alpina (L.)
Curlew	Numenius arquata (L.)
Whimbrel	Numenius phaeopus (L.)

Snipe	Gallinago gallinago (L.)
Great Skua	Catharacta skua skua (Brünn.)
Brown Skua	Catharacta skua lönnbergi (Mathews)
South Polar Skua	Catharacta maccormicki (Saunders)
Pomarine Skua	Stercorarius pomarinus (Temm.)
Arctic Skua	Stercorarius parasiticus (L.)
Long-tailed Skua	Stercorarius longicaudus (Vieill.)
Black-headed Gull	Larus ridibundus (L.)
California Gull	Larus californicus (Brehm)
Lesser Black-backed Gull	Larus fuscus (L.)
Herring Gull	Larus argentatus (Pontopp.)
Glaucous Gull	Larus hyperboreus (Gunn.)
Great Black-backed Gull	Larus marinus (L.)
Common Gull	Larus canus (L.)
Kittiwake	Rissa tridactyla (L.)
Sandwich Tern	Sterna sandvicensis (Lath.)
Common Tern	Sterna hirundo (L.)
Arctic Tern	Sterna paradisaea (Pontopp.)
Roseate Tern	Sterna dougalli (Mont.)
Sooty Tern	Sterna fuscata (L.)
Little Auk	Alle alle (L.)
Great Auk	Alca impennis (L.)
Razorbill	Alca torda (L.)
Guillemot	Uria aalge (Pontopp.)
Black Guillemot	Cepphus grylle (L.)
Puffin	Fratercula arctica (L.)
Woodpigeon	Columba palumbus (L.)
Rock Dove	Columba livia (Gm.)
Cuckoo	Cuculus canorus (L.)
Skylark	Alauda arvensis (L.)
Meadow Pipit	Anthus pratensis (L.)
Wheatear	Oenanthe oenanthe (L.)
Crossbill	Loxia curvirostra (L.)
Starling	Sturnus vulgaris (L.)
Hooded Crow	Corvus corone cornix (L.)
Raven	Corvus corax (L.)

APPENDIX 1. continued.

FISH		
	Pilchard	Sardina pilchardus (Walbaum)
	Haddock	Melanogrammus aeglefinus (L.)
	Whiting	Merlangius merlangus (L.)
	Blue Whiting	Micromesistius poutassou (Risso)
	Norway Pout	Trisopterus esmarkii (Nilsson)
	Sandeel	Ammodytes sp.
	Redfish	Sebastes marinus (L.)
	Plaice	Pleuronectes platessa (L.)
MAMMALS		
	Grey Seal	Halichoerus grypus (Fab.)
	Sheep	Ovis aries (L.)
	Hedgehog	Erinaceus europaeus (L.)
	Blue Hare	Lepus timidus (L.)
	Rabbit	Oryctolagus cuniculus (Lilljeborg)
INVERTEBRATES		
	Mussel	Mytelus edulis (L.)
	Barnacle	Lepas sp.
	Cranefly	Tipula sp.
	Broom Moth	Mamestra pisi (L.)
PLANTS		
	Crowberry	Empetrum nigrum (L.)

APPENDIX 2. Estimates of numbers of pairs of Great Skuas on Foula.

Year	Pairs	Authority	notes
1774	7	Low (1879)	protected by local people
1804	30	Baxter & Rintoul (1953)	
1821	30	Vetch (1822)	some persecution
1850	6	Holbourn (diaries)	many shot
1860	3	Holbourn (diaries)	still being shot
1883	15	Tudor (1883)	protected
1884	16	Evans & Buckley (1899)	probably underestimated
1887	60	Evans & Buckley (1899)	overestimated by Evans
1889	84	Barrington (1890)	inflated by skin-collector
1890	80	Barrington (1890)	inflated by skin-collector
1890	40	Clarke (1894)	nest count (eggs taken)
1891	60	Raeburn (1891)	inflated by skin-collector
1899	17	Holbourn (diaries)	end of persecution
1906	29	Holbourn (diaries)	
1938	250	Venables & Venables (1955)	
1948	350	Pennie (1948)	
1951	600	Fisher & Lockley (1954)	
1956	500	Brathay	August count so too low
1958	1000	Perdeck (1960)	
1963	900	Brathay	probably underestimated
1969	1800	Brathay	
1973	2500		Lincoln Index derivation
1974	2131		count of occupied territories
1974	2500		Lincoln Index derivation
1975	3000		territory count less bias
1976	3000		territory count less bias

APPENDIX 3. Estimates of numbers of pairs of Great Skuas on Unst.

Year	number pairs at Hermaness	Saxavord	Authority	notes
1774	0	3	Low (1879)	
1780's	0	0	Venables & Venables (1955)	
1831	3	0	Venables & Venables (1955)	protected
1850	30	0	Bannerman (1963)	protected
1861	6	0	Gordon (1964)	many shot
1871	5	0	Venables & Venables (1955)	
1884	5	0	Venables & Venables (1955)	still some shooting
1885	6	0	Venables & Venables (1955)	
1886	6	0	Venables & Venables (1955)	
1887	8	0	Venables & Venables (1955)	
1888	8	1	Venables & Venables (1955)	
1889	8	1	Venables & Venables (1955)	
1890	8	1	Venables & Venables (1955)	
1891	8	1	Venables & Venables (1955)	
1892	9	-	Venables & Venables (1955)	
1895	7	-	Venables & Venables (1955)	
1897	20	3	Venables & Venables (1955)	coincides with crash
1898	12	2	Venables & Venables (1955)	of Foula numbers
1905	30	5	Baxter & Rintoul (1953)	
1907	42	-	Cramp et al. (1974)	
1922	60	40	Pitt (1922)	
1925	90	-	Glegg (1926)	
1939	90	30	Rankin (1947)	
1939	100	100	Gordon (1964)	
1949	250	50	Gordon (1964)	
1950	250	50	Lockie (1950)	
1958	340	-	Eggeling (1958)	
1965	300	-	Dott (1967)	underestimate
1969	300	100	Cramp et al. (1974)	underestimate
1974	700	-	Frost (in litt.)	
1974	770	305	Bundy (1974)	
1974	786	-	Albon et al. (1976)	739 nests found
1975	800	300		territory count less bias

APPENDIX 4. Estimates of numbers of Great Skua pairs at Ronas Hill and the rest of Shetland north mainland.

Year	Pairs	Authority	notes
1828	1	Drosier (1831)	
1832	5	Evans & Buckley (1899)	
1837	0	Venables & Venables (1955)	exterminated by Dunn
1881	1	Evans & Buckley (1899)	
1888	4	Evans & Buckley (1899)	
1890	16	Evans & Buckley (1899)	
1900	3	Cramp *et al.* (1974)	
1922	3	Baxter & Rintoul (1953)	
1950	20	Cramp *et al.* (1974)	
1952	28	Venables & Venables (1955)	
1969	7	Cramp *et al.* (1974)	underestimates
1974	220	Everett (1977)	

APPENDIX 5. Estimates of numbers of Great Skua pairs on Yell.

Year	Pairs	Authority	notes
1890	1	Cramp *et al.* (1974)	
1923	2	Glegg (1926)	
1932	56	Yeates (1948)	
1946	96	Yeates (1948)	
1969	125	Cramp *et al.* (1974)	
1974	120		underestimated
1975	257	Everett (1977)	

APPENDIX 6. Estimates of numbers of Great Skua pairs on Fetlar.

Year	Pairs	Authority	notes
1900	1	Cramp *et al.* (1974)	
1946	25	Yeates (1948)	
1950	15	Venables & Venables (1955)	
1952	25	Venables & Venables (1955)	
1969	275	Cramp *et al.* (1974)	
1975	280		territory count less bias
1975	237	Everett (1977)	

APPENDIX 7. Estimates of numbers of Great Skua pairs on Noss.

Year	Pairs	Authority	notes
1910	2	Perry (1948)	
1922	12	Clegg (1926)	
1923	14	Perry (1948)	
1924	15	Perry (1948)	
1926	20	Baxter & Rintoul (1953)	
1928	30	Perry (1948)	
1929	30	Venables & Venables (1955)	
1932	50	Venables & Venables (1955)	
1934	69	Perry (1948)	
1938	80	Perry (1948)	
1939	95	Perry (1948)	
1946	113	Perry (1948)	all nests marked
1952	165	Venables & Venables (1955)	
1955	220	Gordon (1964a)	
1957	200	Gordon (1964a)	
1969	210	Cramp *et al.* (1974)	
1972	200	RSPB reserve report	
1973	230	RSPB reserve report	
1974	242	Kinnear (1974)	all nests marked
1975	250		territory count less bias
1975	255	Everett (1977)	

APPENDIX 8. Estimates of numbers of Great Skua pairs on Hascosay.

Year	Pairs	Authority
1913	4	RSPB reserve report
1932	65	Yeates (1948)
1948	35	Cramp *et al.* (1974)
1952	75	Cramp *et al.* (1974)
1969	40	Cramp *et al.* (1974)
1972	50	RSPB reserve report
1974	55	Everett (1977)

APPENDIX 9. Estimates of numbers of Great Skua pairs on Bressay.

Year	Pairs	Authority	notes
1913	1	Perry (1948)	
1914	1	Perry (1948)	
1946	20	Perry (1948)	
1969	92	Cramp *et al.* (1974)	
1974	175		territory count less bias
1975	160	Everett (1977)	

APPENDIX 10. Estimates of numbers of Great Skua pairs on Hoy.

Year	Pairs	Authority
1914	1	Venables & Venables (1955)
1915	1	Bannerman (1963)
1916	1	Bannerman (1963)
1917	1	Bannerman (1963)
1921	4	Baxter & Rintoul (1953)
1922	3	Baxter & Rintoul (1953)
1923	2	Baxter & Rintoul (1953)
1925	2	Baxter & Rintoul (1953)
1933	8	Baxter & Rintoul (1953)
1941	20	Baxter & Rintoul (1953)
1961	70	Parslow (1967)
1974	400	Beaman (in litt.)
1975	462	Everett (1977)
1975	503	Booth (in litt.)

APPENDIX 11. Estimates of numbers of Great Skua pairs on Fair Isle.

Year	Pairs	Authority	notes
1804	1	Neill (1806)	probably erroneous
1821	0	Venables & Venables (1955)	
1921	1	Williamson (1957)	
1930	3	Williamson (1957)	
1936	3	Williamson (1957)	
1943	1	Williamson (1957)	
1944	1	Williamson (1957)	
1946	2	Williamson (1957)	
1948	4	Williamson (1957)	
1949	4	Williamson (1957)	
1950	6	Williamson (1957)	
1951	5	Williamson (1957)	
1952	10	Williamson (1957)	
1953	9	Williamson (1957)	breeding birds shot by
1954	8	Williamson (1957)	local inhabitants in
1955	13	Williamson (1957)	these years
1956	17	Williamson (1957)	
1957	21	FIBO Bull.	
1958	17	FIBO Bull.	
1959	19	FIBO Bull.	
1960	20	FIBO Bull.	
1961	20	FIBO Bull.	
1962	25	FIBO Bull.	
1963	31	FIBO Bull.	
1964	20	FIBO Bull.	breeding birds shot
1965	12	FIBO Bull.	by local inhabitants
1966	18	FIBO Bull.	over these years
1967	12	FIBO Bull.	" "
1968	10	FIBO Bull.	" "
1969	8	FIBO Bull.	" "
1970	8	FIBO Bull.	" "
1971	12	FIBO Bull.	
1972	13	FIBO Bull.	
1973	13	FIBO Bull.	
1974	17	FIBO Bull.	
1975	21	FIBO Bull.	
1976	25	FIBO Bull.	

APPENDIX 12. Estimates of numbers of Great Skua pairs on Mousa.

Year	Pairs	Authority
1925	2	Clegg (1926)
1928	3	Cramp et al. (1974)
1949	3	Venables & Venables (1955)
1950	3	Venables & Venables (1955)
1951	4	Venables & Venables (1955)
1969	12	Cramp et al. (1974)
1972	20	RSPB reserve report
1974	9	Everett (1977)

APPENDIX 13. Estimates of numbers of Great Skua pairs at Fitful Head.

Year	Pairs	Authority
1925	2	Clegg (1926)
1948	3	Venables & Venables (1955)
1949	3	Venables & Venables (1955)
1951	5	Venables & Venables (1955)
1952	5	Venables & Venables (1955)
1969	13	Cramp et al. (1974)
1974	50	Everett (1977)

APPENDIX 14. Estimates of numbers of Great Skua pairs on Lewis.

Year	Pairs	Authority
1945	1	Parslow (1967)
1959	3	Cunningham (1959)
1964	4	Scottish Birds Editorial (1964)
1969	10	Cramp et al. (1974)
1974	13	Everett (1977)

APPENDIX 15. Estimates of numbers of Great Skua pairs on Vaila.

Year	Pairs	Authority
1948	1	Venables & Venables (1955)
1950	2	Cramp *et al.* (1974)
1969	6	Cramp *et al.* (1974)
1974	9	Everett (1977)

APPENDIX 16. Estimates of numbers of Great Skua pairs on Urie Lingey.

Year	Pairs	Authority
1950	2	Cramp *et al.* (1974)
1969	2	Cramp *et al.* (1974)

APPENDIX 17. Estimates of numbers of Great Skua pairs on Papa Westray.

Year	Pairs	Authority
1950	2	Bannerman (1963)
1953	2	Tewnion (1958)
1961	5	Balfour (1968)
1969	6	Cramp *et al.* (1974)
1974	4	Everett (1977)

APPENDIX 18. Estimates of numbers of Great Skua pairs at Dunnet Head.

Year	Pairs	Authority
1950	1	Venables & Venables (1955)
1974	1	Everett (1977)

APPENDIX 19. Estimates of numbers of Great Skua pairs on Tronda.

Year	Pairs	Authority
1951	1	Venables & Venables (1955)
1952	1	Cramp et al. (1974)
1969	0	Cramp et al. (1974)

APPENDIX 20. Estimates of numbers of Great Skua pairs on Gluss Isle.

Year	Pairs	Authority
1952	2	Cramp et al. (1974)
1969	1	Cramp et al. (1974)

APPENDIX 21. Estimates of numbers of Great Skuas on Rousay.

Year	Pairs	Authority
1955	1	Bannerman (1963)
1957	2	Bannerman (1963)
1958	2	Bannerman (1963)
1961	2	Bannerman (1963)
1961	6	Balfour (1968)
1974	5	Everett (1977)

APPENDIX 22. Estimates of numbers of Great Skua pairs on Eynhallow.

Year	Pairs	Authority
1956	1	Bannerman (1963)
1961	1	Balfour (1968)
1974	0	Everett (1977)

APPENDIX 23. Estimates of numbers of Great Skua pairs on Westray.

Year	Pairs	Authority
1958	1	Bannerman (1963)
1961	1	Balfour (1968)

APPENDIX 24. Estimates of numbers of Great Skua pairs on St Kilda.

Year	Pairs	Authority
1962	1	Pollock (1963)
1969	8	Cramp et al. (1974)
1971	10	Flegg (1972)
1974	10	Everett (1977)

APPENDIX 25. Estimates of numbers of Great Skua pairs on North Rona.

Year	Pairs	Authority
1964	2	Scottish Birds Editorial (1964)
1965	2	Robson (1968)
1972	3	Evans (1975)

APPENDIX 26. Estimates of numbers of Great Skua pairs on Handa.

Year	Pairs	Authority
1964	1	Parslow (1967)
1965	1	RSPB reserve report
1966	2	RSPB reserve report
1967	3	RSPB reserve report
1968	3	RSPB reserve report
1969	3	RSPB reserve report
1970	3	RSPB reserve report
1971	3	RSPB reserve report
1972	4	RSPB reserve report
1973	5	RSPB reserve report
1974	7	RSPB reserve report

APPENDIX 27. Estimates of numbers of Great Skua pairs at other colonies in Britain.

Colony	Year	Pairs	Authority
Sanday	1961	1	Bannerman (1963)
Eday	1969	1	Cramp *et al.* (1974)
	1974	1	Everett (1977)
Auskerry	1973	2	Everett (1977)
	1974	2	Everett (1977)
Birsay	1974	4	Everett (1977)
Stronsay	1974	3	Everett (1977)
Calf of Eday	1974	1	Everett (1977)

APPENDIX 28. Numbers of otoliths of each fish species taken at fishing boats by Great Skuas (prebreeders at club sites) through the 1975 season on Foula.

Date	number of otoliths	Norway Pout	Haddock	Whiting	Redfish	Blue Whiting	Plaice
13.4	4	4	0	0	0	0	0
28.5	104	30	44	29	1	0	0
24.6	198	41	97	59	1	0	0
4.7	131	27	55	45	4	0	0
10.7	137	27	50	59	1	0	0
20.7	62	30	16	16	0	0	0
25.7	126	34	33	59	0	0	0
1.8	154	46	57	50	0	1	0
5.8	47	5	23	19	0	0	0
10.8	119	35	32	52	0	0	0

APPENDIX 29. Numbers of otoliths of each fish species taken at fishing boats by Great Skuas (prebreeders at club sites) through the 1976 season on Foula.

Date	number of otoliths	Norway Pout	Haddock	Whiting	Redfish	Blue Whiting	Plaice
10.5	145	27	84	30	0	2	2
20.5	184	19	72	89	4	0	0
31.5	134	12	65	54	1	2	0
10.6	80	6	31	39	0	0	4
20.6	59	19	15	23	0	1	1
30.6	43	6	6	31	0	0	0
10.7	53	8	18	27	0	0	0
20.7	44	7	9	26	0	2	0
30.7	63	14	23	26	0	0	0

APPENDIX 30. Numbers of otoliths of each fish species taken by Great Skuas and collected from territories on Foula in 1976.

Date	number of otoliths	Norway Pout	Haddock	Whiting	Redfish	Blue Whiting	Plaice
10.5	91	16	62	13	0	0	0
20.5	59	9	24	26	0	0	0
31.5	18	1	10	7	0	0	0
10.6	53	0	23	30	0	0	0

APPENDIX 31. Numbers of otoliths of each fish species taken at fishing boats by nonbreeding Great Black-backed Gulls and found in pellets collected at loafing sites on Foula in 1975.

Date	number of otoliths	Norway Pout	Haddock	Whiting	Redfish	Blue Whiting	Plaice
23.6	124	0	70	46	8	0	0
10.7	50	0	24	25	1	0	0
25.7	67	0	31	34	2	0	0

APPENDIX 32. Numbers of otoliths of each fish species taken at fishing boats by nonbreeding Great Black-backed Gulls and found in pellets collected at loafing sites on Foula in 1976.

Date	number of otoliths	Norway Pout	Haddock	Whiting	Redfish	Blue Whiting	Plaice
10.5	29	0	22	7	0	0	0
20.5	20	0	10	10	0	0	0
31.5	59	0	31	22	6	0	0
10.6	27	0	14	11	2	0	0
20.6	171	3	88	65	14	0	1
30.6	66	2	31	25	8	0	0
10.7	61	0	25	31	5	0	0
20.7	100	2	32	57	8	1	0
30.7	96	2	39	50	5	0	0

APPENDIX 33. Seasonal variations in egg parameters measured on Foula in 1975.

Parameters		Time period 4–12.6	13–16.6	17–20.6	21–24.6	25–29.6	30.6–20.7
CLUTCHES OF ONE EGG:							
sample size		6	7	12	8	11	13
length	mean	70·97	72·54	71·82	72·31	69·63	70·98
	se	0·36	0·99	0·85	1·27	0·42	0·88
breadth	mean	49·62	50·70	51·44	49·36	49·66	49·41
	se	0·81	0·52	0·40	0·36	0·22	0·29
shape index	mean	69·89	70·00	71·76	68·45	71·33	69·72
	se	0·89	1·54	1·14	1·40	0·49	0·88
volume	mean	84·03	89·45	91·21	84·56	82·43	83·23
	se	3·17	1·34	1·44	1·57	0·96	1·56
CLUTCHES OF TWO EGGS:							
sample size		57	76	74	48	43	48
FIRST HATCHED:							
length	mean	72·67	72·73	72·58	72·63	72·12	70·99
	se	0·21	0·30	0·30	0·44	0·33	0·36
breadth	mean	50·41	50·22	50·26	49·88	49·53	49·20
	se	0·15	0·13	0·11	0·18	0·18	0·18
shape index	mean	69·43	69·12	69·33	68·78	68·72	69·39
	se	0·33	0·33	0·31	0·47	0·36	0·50
volume	mean	88·70	88·09	88·05	86·82	84·52	82·55
	se	0·63	0·58	0·55	0·85	0·81	0·73
SECOND HATCHED:							
length	mean	70·70	70·49	70·47	69·59	69·12	68·76
	se	0·29	0·29	0·28	0·47	0·37	0·31
breadth	mean	50·52	50·51	50·54	50·05	49·93	49·40
	se	0·15	0·15	0·12	0·20	0·16	0·18
shape index	mean	71·50	71·77	71·76	72·03	72·31	71·91
	se	0·32	0·33	0·31	0·45	0·40	0·40
volume	mean	88·00	86·38	86·45	83·78	82·76	80·60
	se	0·67	0·63	0·59	0·98	0·78	0·72

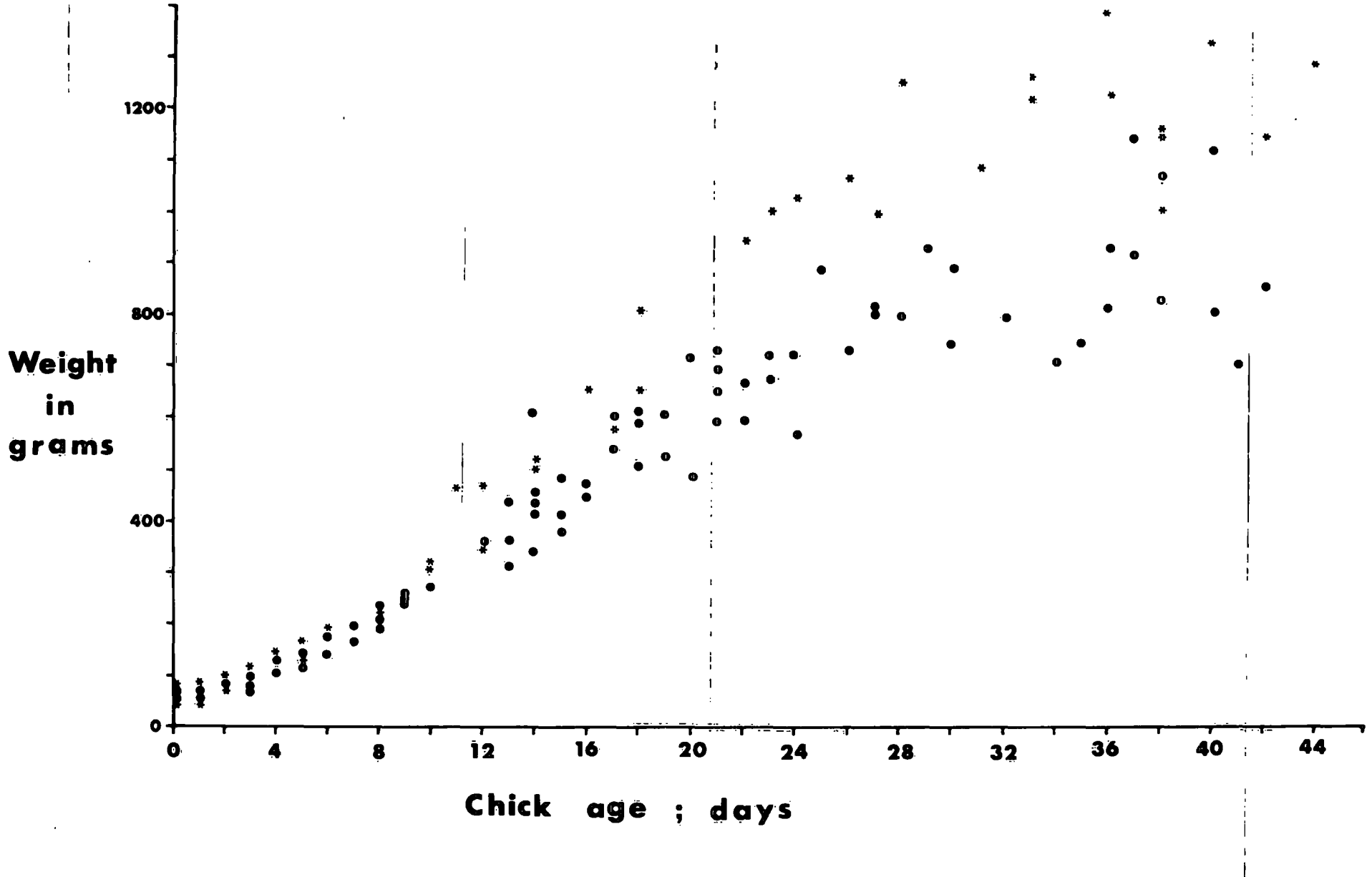
APPENDIX 34. Seasonal variation in egg volumes of clutches measured on Foula in 1976. Egg volume is measured in cm^3 (internal volume).

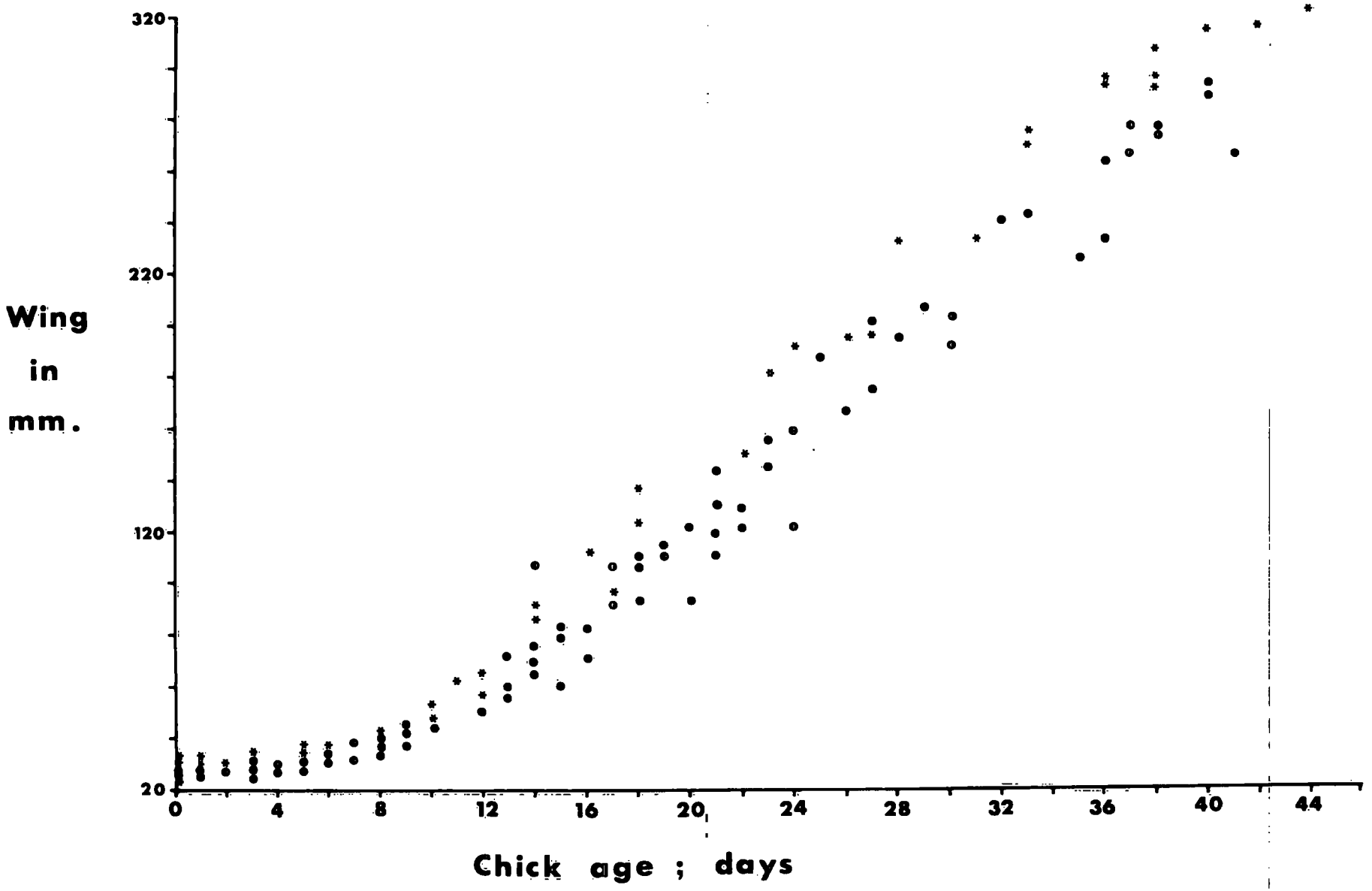
Clutch size and hatching order	Time period					
	4.6–12.6	13–16.6	17–20.6	21–24.6	25.29.6	30.6–20.7
CLUTCHES OF ONE:						
sample size	5	0	5	3	3	10
mean volume	91·31	-	85·51	83·08	83·23	78·71
standard error	1·49	-	3·30	2·96	1·40	3·50
CLUTCHES OF TWO:						
FIRST HATCHED;						
sample size	121	81	56	35	20	32
mean volume	87·37	87·54	87·07	87·40	88·56	83·37
standard error	0·45	0·64	0·75	0·94	0·76	0·94
SECOND HATCHED;						
sample size	121	81	56	35	20	32
mean volume	85·95	85·37	85·17	85·07	85·43	81·31
standard error	0·46	0·70	0·78	1·10	0·72	0·82

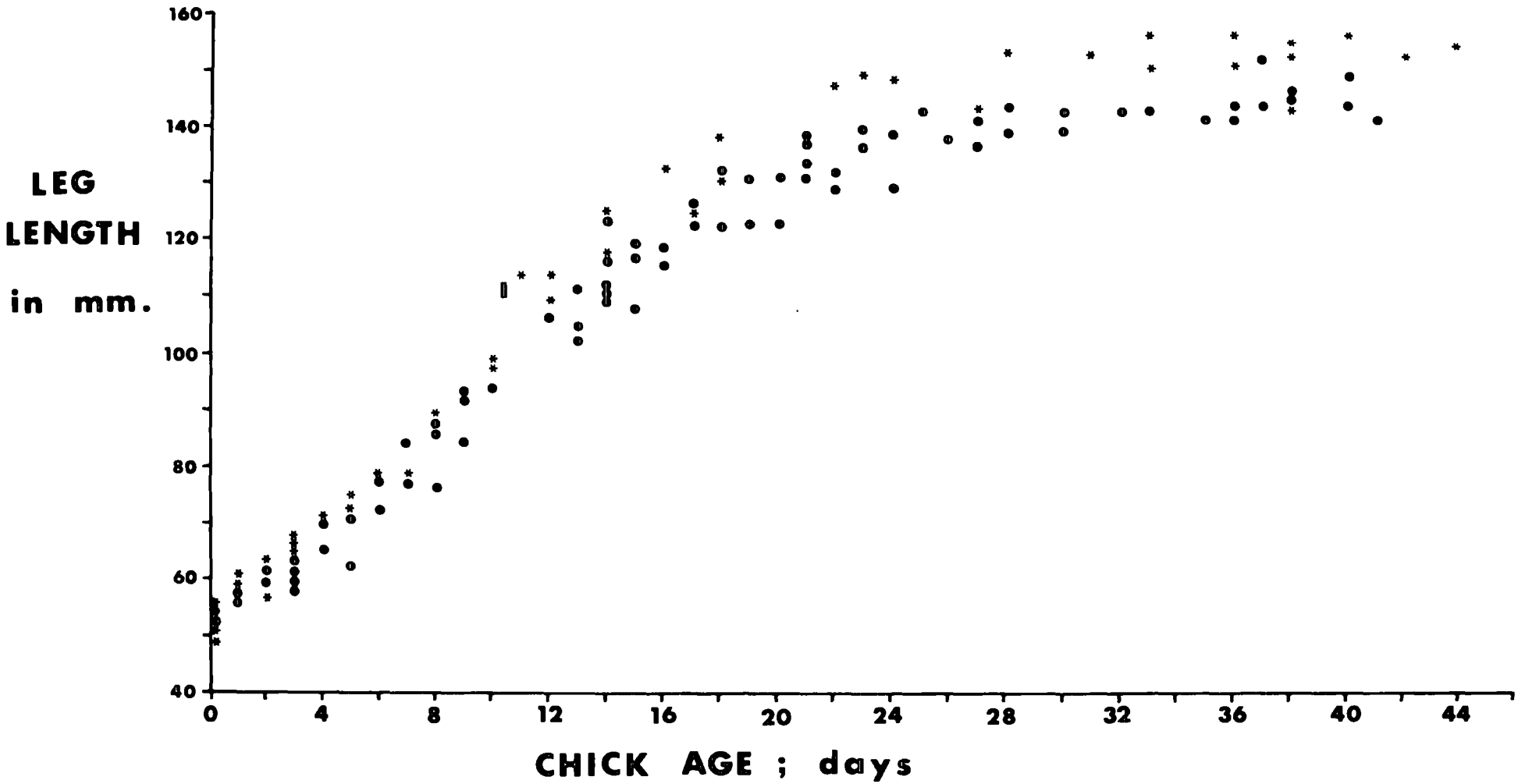
APPENDIX 35. a) Weights of chicks of known ages plotted against chick age. Individual weights of chicks of broods of one, hatched before 10 June in 1975 (*) and second hatched chicks of broods of two, hatched after 26 June in 1975 (•) show the greatest difference in weights in relation to hatching date and chick status.

b) Wing lengths of chicks of known ages plotted against chick age. Categories and symbols as in a).

c) Leg lengths of chicks of known ages plotted against chick age. Categories and symbols as in a).


Weight in grams
1200
800
400
0
0
4
8
12
16
20
24
28
32
36
40
44
Chick age ; days


Wing
in
mm.
320
220
120
20
0
4
8
12
16
20
24
28
32
36
40
44
Chick age ; days


LEG
LENGTH
in mm.
160
140
120
100
80
60
40
0
4
8
12
16
20
24
28
32
36
40
44
CHICK AGE ; days

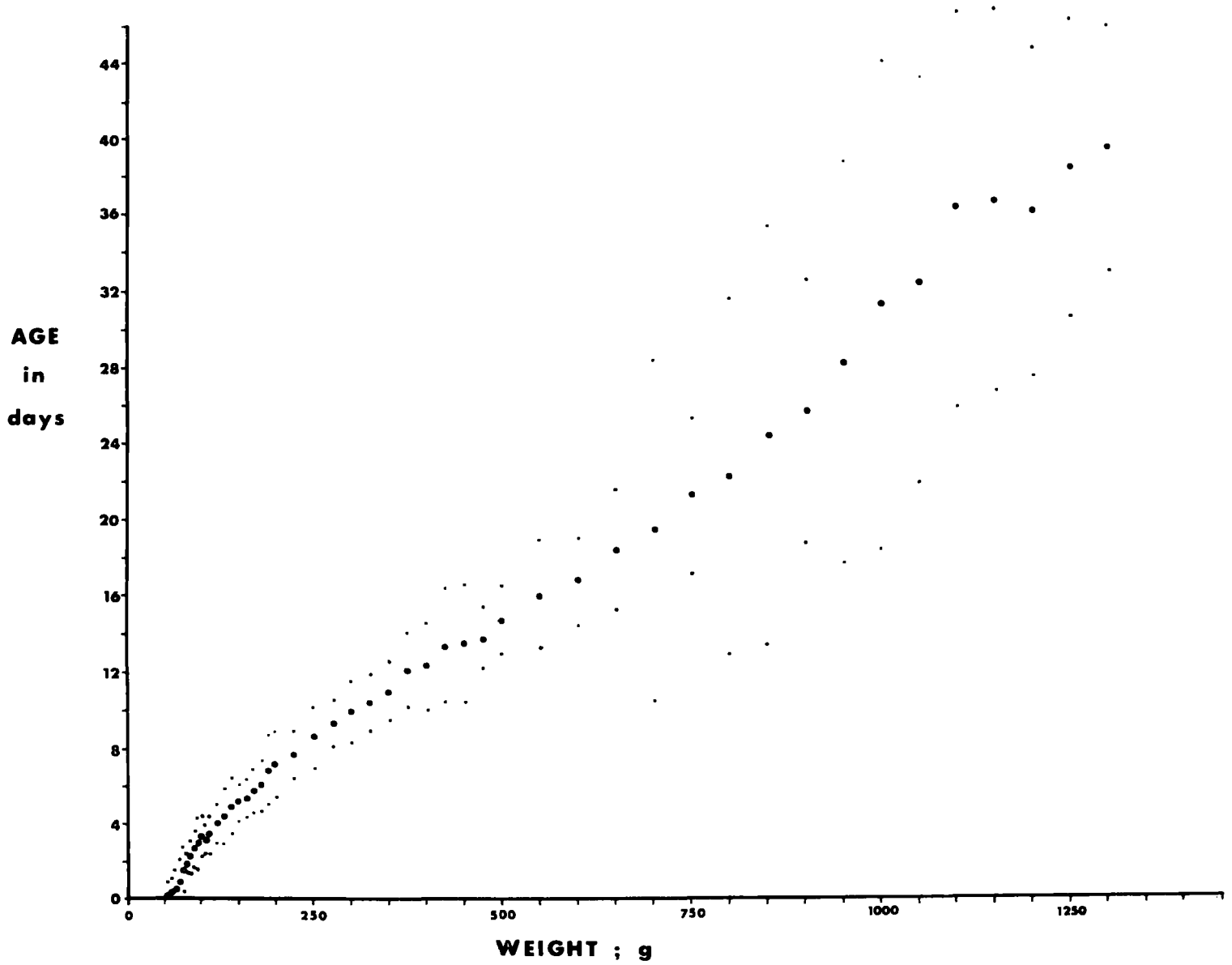
APPENDIX 36. Great Skua chick weights determined by measurement of chicks of known age on Foula in 1975; all chicks.

Age day	sample size	mean weight (g)	standard deviation	standard error	coefficient of variation
0	89	64·5	4·5	0·47	6·9
1	87	69·6	5·3	0·57	7·6
2	82	81·2	7·4	0·82	9·1
3	74	101·2	11·5	1·33	11·3
4	66	125·5	12·9	1·59	9·7
5	73	150·4	17·6	2·06	11·7
6	64	176·8	19·8	2·48	11·2
7	67	205·1	24·3	2·97	11·9
8	47	230·9	28·4	4·15	12·3
9	48	274·4	30·3	4·38	11·0
10	47	322·7	30·7	4·48	9·5
11	38	360·1	44·0	7·14	12·2
12	43	400·2	43·1	6·57	10·8
13	36	436·8	54·9	9·14	12·6
14	57	484·7	52·1	6·90	10·7
15	58	520·6	61·3	8·05	11·8
16	42	577·5	59·2	9·14	10·2
17	50	613·1	78·5	11·10	12·8
18	45	659·8	63·7	9·50	9·7
19	32	695·6	82·7	14·62	11·9
20	34	755·4	101·4	17·39	13·4
21	30	764·3	87·7	16·01	11·5
22	38	819·3	113·0	18·34	13·8
23	41	836·3	110·1	17·20	13·2
24	26	900·6	111·8	21·94	12·4
25	20	952·0	94·3	21·09	9·9
26	29	924·8	118·6	22·02	12·8
27	29	940·7	114·3	21·23	12·1
28	22	990·0	140·7	30·00	14·2
29	30	986·5	85·6	15·64	8·7
30	26	1032·3	107·9	21·15	10·4
31	26	1055·8	105·3	20·66	10·0
32	18	1035·6	131·3	30·95	12·7
33	28	1061·1	117·5	22·20	11·1
34	21	1107·1	87·6	19·11	7·9
35	18	1055·0	127·5	30·06	12·1
36	23	1142·8	150·3	31·35	13·2
37	16	1111·9	126·8	31·70	11·4
38	21	1066·7	115·1	25·11	10·8
39	18	1080·6	103·8	24·48	9·6
40	22	1087·7	141·8	30·22	13·0
41	11	1010·0	172·3	51·94	17·1
42	13	1050·0	144·6	40·10	13·8
43	11	1066·4	161·9	48·81	15·2
44	11	1136·4	97·3	28·99	8·6
45	10	1094·0	129·2	40·86	11·8

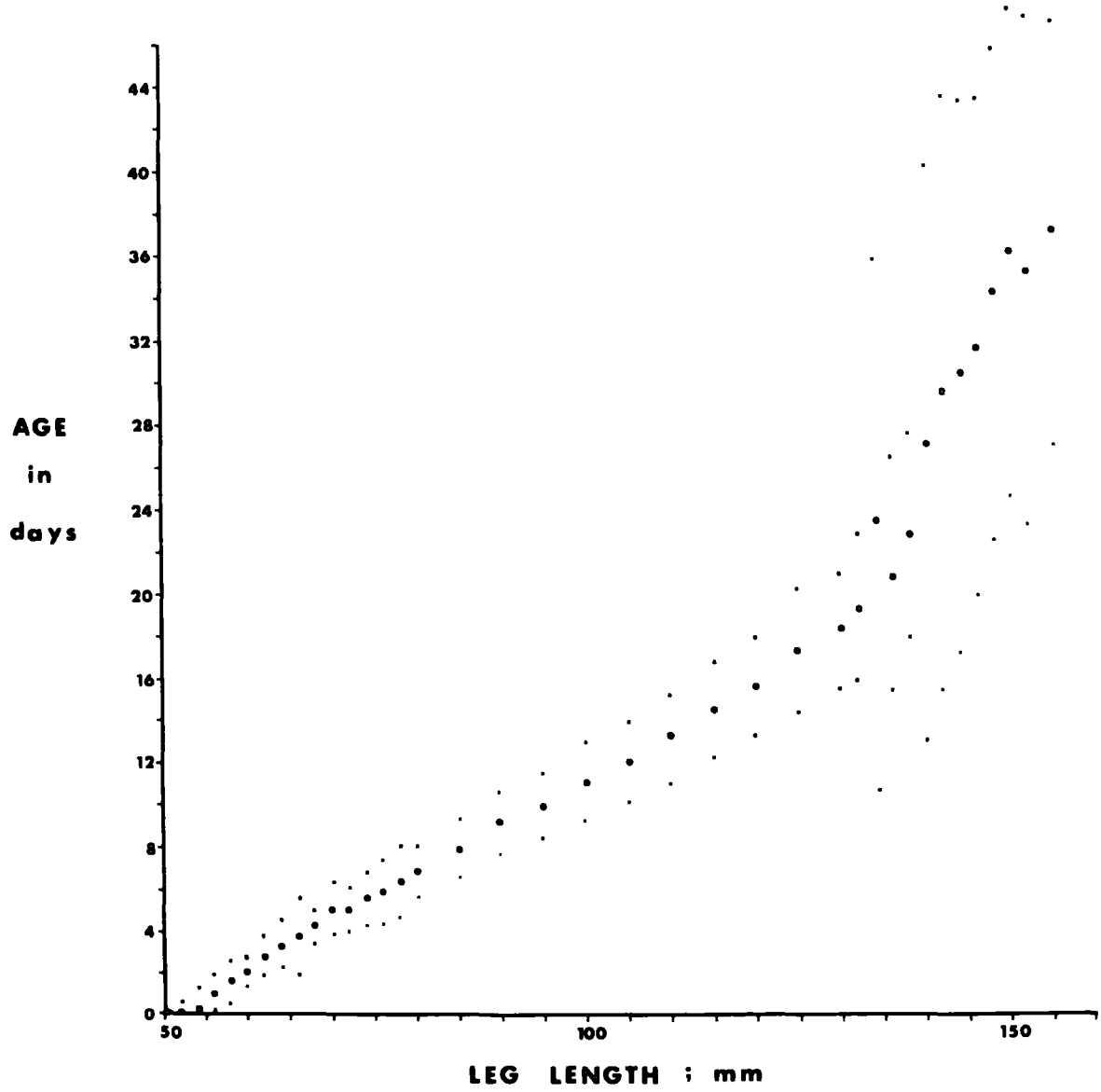
APPENDIX 37. Weight, wing and leg length of chicks aged 0 to 45 days, hatched in 1975vat Foula before 21 June. These are defined as "typical" Great Skua chick growth data for Shetland.

Age day	sample size	Weight (g) mean	se	cv	Wing (mm) mean	se	cv	Leg (mm) mean	se	cv
0	69	65·1	0·5	6·6	24·7	0·18	5·9	52·5	0·26	4·0
1	67	69·8	0·5	6·4	25·9	0·15	4·7	56·6	0·16	2·3
2	58	80·2	0·8	7·5	27·0	0·16	4·7	59·5	0·20	2·6
3	53	101·6	1·4	9·8	28·1	0·18	4·6	64·1	0·25	2·8
4	48	124·8	1·8	10·2	30·1	0·18	4·1	67·5	0·29	3·0
5	53	153·6	2·1	9·8	32·1	0·25	5·7	72·6	0·41	4·1
6	50	176·3	2·8	11·3	33·8	0·27	5·7	76·3	0·49	4·6
7	45	204·4	3·8	12·6	35·7	0·41	7·6	81·5	0·77	6·3
8	34	238·2	4·2	10·4	38·1	0·38	5·8	86·9	0·61	4·1
9	33	272·8	5·2	10·9	40·7	0·50	7·1	91·8	0·68	4·2
10	37	323·4	5·3	10·1	46·2	0·60	7·9	97·9	0·63	3·9
11	30	365·5	7·1	10·7	50·8	0·94	10·1	102·8	0·77	4·1
12	34	402·7	7·4	10·7	57·5	0·98	10·0	107·4	0·67	3·6
13	27	455·6	7·6	8·7	66·9	1·55	12·0	112·6	0·82	3·8
14	39	498·3	7·1	8·8	76·7	0·91	7·4	116·4	0·67	3·6
15	38	535·0	9·0	10·3	83·3	1·38	10·3	119·5	0·66	3·4
16	32	590·7	9·0	8·6	92·7	1·52	9·3	124·2	0·70	3·2
17	35	640·1	10·5	9·7	101·9	1·67	9·7	126·9	0·66	3·1
18	37	673·8	9·4	8·5	113·5	1·70	9·1	129·6	0·58	2·7
19	21	716·9	16·7	10·7	123·0	1·95	7·2	131·9	1·08	3·8
20	23	795·9	15·3	9·2	135·9	1·56	5·5	136·4	1·04	3·7
21	19	803·2	16·4	8·9	146·1	3·11	9·3	137·6	0·91	2·9
22	28	860·4	15·8	9·8	151·4	1·68	5·9	140·0	0·75	2·8
23	27	882·2	17·1	10·1	163·4	1·99	6·3	140·9	0·79	3·0
24	18	927·5	19·6	9·0	177·5	2·85	6·8	142·1	1·01	3·0
25	17	971·8	21·1	8·9	186·6	2·24	5·0	144·4	0·81	2·3
26	16	999·4	14·4	5·8	197·6	1·25	2·5	145·8	1·02	2·8
27	18	988·3	20·1	8·6	199·8	2·23	4·7	145·2	0·85	2·5
28	15	1057·3	21·9	8·0	212·7	2·41	4·4	145·3	0·77	2·0
29	21	1011·2	13·1	5·9	220·0	1·37	2·8	145·1	0·72	2·3
30	20	1056·5	19·6	8·3	231·2	1·69	3·3	146·5	0·51	1·6
31	20	1086·5	14·7	6·1	236·8	1·48	2·8	147·5	0·79	2·4
32	11	1090·9	37·2	11·3	247·1	2·82	3·8	146·3	1·38	3·1
33	20	1107·0	18·9	7·6	250·6	4·86	8·7	147·4	0·79	2·4
34	16	1116·2	21·6	7·7	256·9	5·01	7·8	145·8	0·94	2·6
35	12	1100·8	28·3	8·9	270·0	1·73	2·2	145·9	0·88	2·1
36	17	1195·6	28·3	9·8	279·6	2·67	3·9	149·1	0·95	2·6
37	10	1183·0	22·9	6·2	287·1	1·88	2·1	147·2	1·01	2·2
38	16	1100·6	25·5	9·3	289·0	2·99	4·0	146·8	1·30	3·6
39	15	1115·3	17·9	6·2	296·3	2·13	2·8	146·6	0·82	2·2
40	13	1160·8	26·8	8·3	300·8	2·07	2·5	147·9	1·14	2·8
41	5	1144·0	34·9	6·8	305·6	3·04	2·2	144·8	1·74	2·7
42	12	1056·7	43·0	14·1	304·7	2·38	2·7	148·0	1·31	3·1
43	7	1142·9	52·9	12·2	305·4	7·22	6·2	148·4	0·88	1·7
44	10	1143·0	31·6	8·7	313·7	1·26	1·3	148·8	1·05	2·2
45	9	1101·1	44·9	12·2	310·2	5·10	4·9	147·6	1·34	2·7

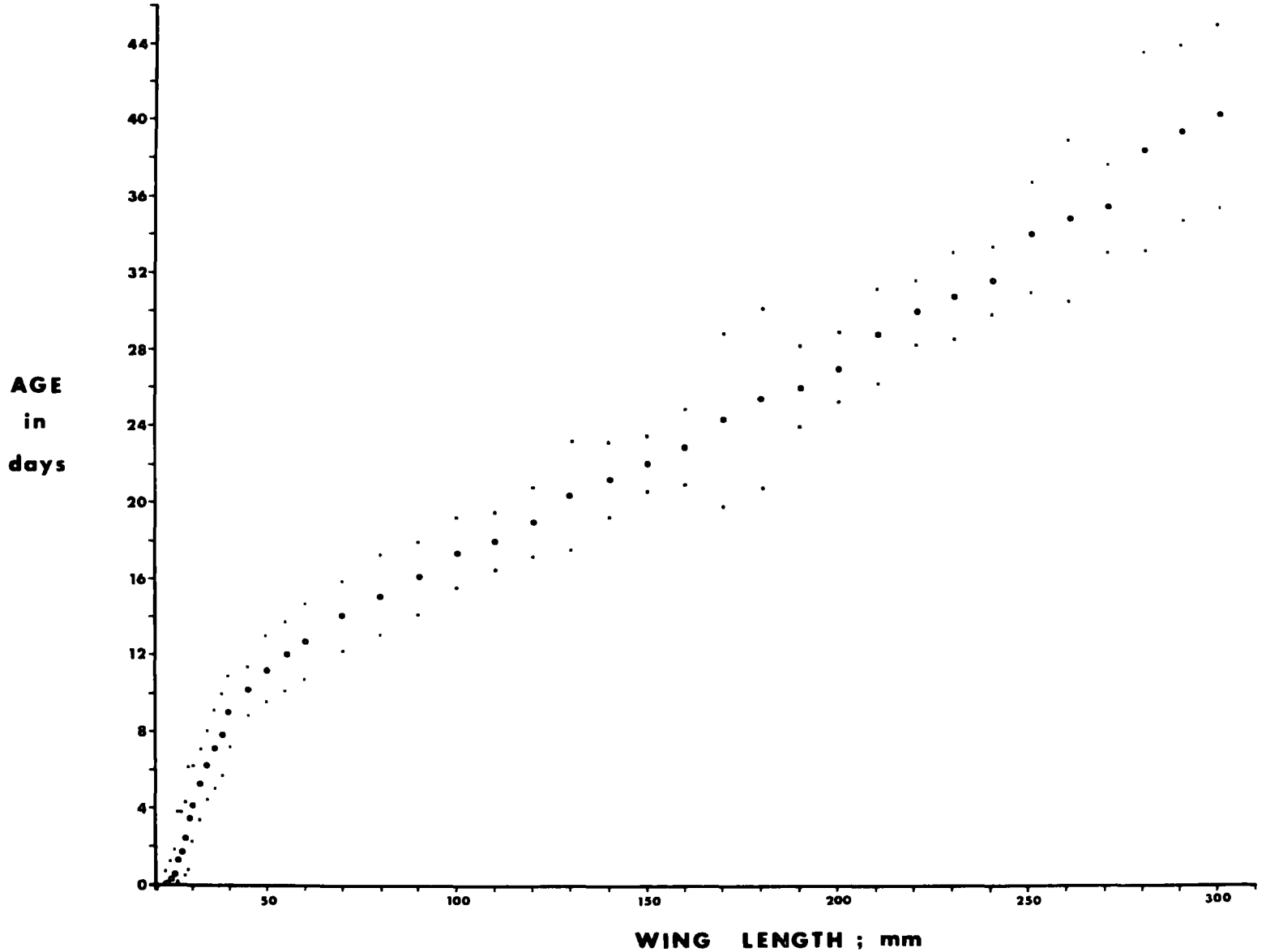
APPENDIX 38. Mean ages of chicks of known age hatched before 20 June in 1975 (growing "typically") in relation to their weights. Mean ages are marked by • and the 95% confidence limits for individual ages by * .


AGE
in
days
0
4
8
12
16
20
24
28
32
36
40
44
0
250
500
750
1000
1250
WEIGHT ; g

APPENDIX 39. Mean ages of chicks of known age hatched before 20 June in 1975 (growing "typically") in relation to their leg lengths. Mean ages are marked by • and the 95% confidence limits for individual ages by * .


AGE
in
days
44
40
36
32
28
24
20
16
12
8
4
0
50
100
150
LEG LENGTH ; mm

APPENDIX 40. Mean ages of chicks of known age hatched before 20 June in 1975 (growing "typically") in relation to their wing lengths. Mean ages are marked by • and the 95% confidence limits for individual ages by * .


AGE
in
days
0
4
8
12
16
20
24
28
32
36
40
44
50
100
150
200
250
300
WING LENGTH ; mm

APPENDIX 41. Table of conversions from chick leg lengths to age for Great Skua chicks in British colonies growing "typically".

Leg length (mm)	Chick age (days)
54	0
55	1
56	1
57	1
58	2
59	2
60	2
61	2
62	3
63	3
64	3
65	3
66	4
67	4
68	4
69	4
70	5
71	5
72	5
73	5
74	6
75	6
76	6
77	6
78	6
79	7
80	7
81	7
82	7
83	7
84	8
85	8
86	8
87	8
88	9
89	9
90	9
91	9
92	9
93	10
94	10
95	10
96	10
97	10
98	11
99	11
100	11
101	11
102	11
103	12
104	12
105	12
106	12
107	13
108	13
109	13
110	13
111	13
112	14
113	14
114	14
115	14
116	15
117	15
118	15
119	15
120	16
121	16
122	16
123	16
124	17
125	17
126	17
127	18
128	18
129	18
130	18
131	19
132	19
133	20
134	20
135	20

leg lengths greater than 135 mm cannot be accurately converted to chick age.

APPENDIX 42. Table of conversions from chick wing length to age for Great Skua chicks growing "typically" in British colonies.

Range of wing lengths (mm)	Chick age (days)	Range of wing lengths (mm)	Chick age (days)
21 - 25	0	173 -181	25
26	1	182 -190	26
27 - 28	2	191 -200	27
29	3	201 -210	28
30	4	211 -219	29
31 - 32	5	220 -229	30
33	6	230 -238	31
34 - 36	7	239 -247	32
37 - 38	8	248 -255	33
39 - 42	9	256 -262	34
43 - 46	10	263 -269	35
47 - 51	11	270 -275	36
52 - 58	12	276 -281	37
59 - 66	13	282 -287	38
67 - 75	14	288 -294	39
76 - 85	15	295 -298	40
86 - 95	16	299 -303	41
96 -104	17	304 -307	42
105 -114	18	308 -313	43
115 -123	19	314 -318	44
124 -133	20	319 -325	45
134 -143	21	326 -330	46
144 -152	22	331 -334	47
153 -162	23	335 -345	48
163 -172	24		

APPENDIX 43. Weights of chicks in relation to their wing length. Data from chicks of known age measured on Foula in 1975; hatching dates before 20 June ("typical" growth).

Wing length (mm)	sample size	mean weight	standard deviation	standard error
20 - 24	35	64·5	4·2	0·7
25 - 29	218	82·3	18·5	1·3
30 - 34	134	149·2	27·6	2·4
35 - 39	92	216·3	29·1	3·0
40 - 44	46	288·6	33·7	5·0
45 - 49	24	329·8	29·2	6·0
50 - 59	57	385·4	35·9	4·8
60 - 69	23	447·0	40·7	8·5
70 - 79	52	492·8	47·7	6·6
80 - 89	37	535·2	46·2	7·6
90 - 99	39	598·7	49·5	7·9
100-109	32	655·8	44·8	7·9
110-119	25	671·6	42·8	8·6
120-129	27	715·9	55·8	10·7
130-139	24	759·4	58·9	12·0
140-149	23	838·6	51·5	10·7
150-159	25	871·0	81·9	16·4
160-169	20	877·5	68·6	15·3
170-179	19	918·4	60·2	13·8
180-189	16	970·0	82·4	20·6
190-199	28	997·7	62·9	11·9
200-209	14	989·3	66·3	17·7
210-219	24	1017·9	70·2	14·3
220-229	23	1034·3	69·9	14·6
230-239	23	1078·0	74·0	15·4
240-249	16	1090·6	77·9	19·5
250-259	18	1093·9	97·3	22·9
260-269	24	1122·1	95·0	19·4
270-279	17	1168·5	84·8	20·6
280-289	19	1145·8	97·9	22·5
290-299	32	1108·8	125·2	22·1
300-309	17	1116·5	109·4	26·5
310-319	27	1160·0	107·3	20·7
320-329	6	1188·3	58·8	24·0